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AN ECOLOGICAL STUDY OF THE PASTURE SCARAB *APHODIUS HOWITTI* HOPE

By P. B. CARNE*

CONTENTS

* Division of Entomology, C.S.I.R.O., Canberra, A.C.T.

Summary

The larval stage of *Aphodius howitti* Hope is a pest of improved and sown pastures in south-eastern Australia. The great increase in pasture improvement and of stocking rates over the past 25-30 years have favoured the development of high numbers of this insect, largely because of its preference for leguminous pasture species, especially subterranean clover (*Trifolium subterraneum* L.).

This paper describes a general study of the life-cycle, behaviour, food, and oviposition site preferences of the species and includes a discussion of the mortality factors likely to be of significance in regulating its numbers.

The species has an annual life-cycle. Studies on its biology revealed that adult females lay two distinct batches of eggs. The larger batch (*c.* 35 eggs) is laid before the female feeds in dung, sometimes even before flight; the smaller (*c.* 15 eggs), after feeding. The presence of dung is therefore not necessary for the survival of the species which is often found at high densities in ungrazed turf.

The factors initiating and influencing flight activity were studied in detail. Initiation is triggered by light of a particular intensity; the time of appearance of beetles in flight can be forecast accurately in relation to the time of sunset. Flights are favoured by high temperature, high soil moisture, and by low wind velocity. Unfed beetles fly upwind towards dung pads. Gravid females execute a circling, exploratory flight; they appear to seek out comparatively bare situations for oviposition and usually enter the soil through small cracks such as are made by germinating clover plants.

When weather conditions are unfavourable for flight, females may oviposit *in situ*. This may account for the observed tendency for particular sites to support dense populations for several successive seasons. Under more favourable conditions most of the females fly before ovipositing; these and females ovipositing for a second time may select previously unoccupied sites for oviposition. In all samples of adults, females outnumbered males; even samples of insectary-reared pupae showed similar inequality in the same direction.

The larvae move freely on the surface at night when weather conditions are favourable. They move at random, excavating new burrows when they find suitable plants or pieces of dung. The soil thrown up by third instar larvae is quite voluminous and may almost conceal short pastures. Larval development is most rapid in light textured soils, especially if these are rich in organic matter. A diet of legumes promotes more rapid growth than one of grasses alone. The species appears to be unable to take advantage of temporary amelioration of conditions in districts marginal to its permanent geographical limits of distribution. It may be very abundant locally close to

these limits. In unimproved native pastures it is a rare species, high numbers only being found in or near stock camps.

Whether or not the species occurs in a pasture in large numbers is determined more by the composition and density of the vegetation, than by factors such as soil pH or organic matter content. Very heavy soils are avoided. Recently-established pastures rarely support high numbers, damage being caused only to pastures more than 2-3 yr old.

Populations are very discontinuous in their distribution. The species prefers to oviposit on the upper slopes and tops of rises in undulating country. In exceptionally dry seasons, *slight* depressions are sometimes favoured. Where oviposition has been intense, the larvae move out laterally during their developmental period and accumulate on circular "fronts" about their point of origin. There is a marked tendency for oviposition to be particularly intense about conspicuous objects such as trees and fences. Even in flat, uniform pastures a marked patchiness is often observed. There is, however, no indication that the females fly in swarms when seeking oviposition sites.

Field observations on the distribution and mortality of *Aphodius* suggest that the density regulation of this species is in conformity with a general hypothesis of the regulation of animal populations advanced by Nicholson (1954), whose terminology is therefore adopted.

The major governing factors recognized are density-induced larval combat and fungal diseases such as caused by *Cordyceps aphodii* Mathieson. Combat appears to act as a powerful density-stabilizing mechanism in that irrespective of the initial densities of larvae above a certain critical level — approximately 10 per sq. lk — that of the immature adults produced is approximately constant. Fungal diseases occur in all parts of the range of the host. In patches of high host density the concentration of spores rises to a level sufficient to cause high mortality to larvae of the subsequent generation occupying these sites. This factor may therefore be said to have a tardy type of density reaction.

Other mortality factors include desiccation and drowning of larvae, infection by nematodes (*Mermis* sp.), predation by birds, asilid, and carabid larvae, and parasitism by thynnid wasps (*Tachinomyia* sp.). None of these are considered to contribute significantly to the density regulation of the species.

Purely density legislative factors include the distribution of favourable oviposition sites, a bacterial disease that infects larvae subsequent to their being damaged in combat, and weather factors that directly and indirectly influence the intensity of larval combat.

The development of high numbers is favoured by evenly distributed rainfall during the larval stages. On the Southern Tablelands of New South Wales falls in excess of 4 in. in any month are unfavourable. Large catches of adults in light traps at Canberra followed years in which rainfall was below average, and vice versa. The nature of the pasture damage caused by the species is discussed, and ecological control possibilities examined. The latter include the greater use of hardy perennial pasture species, or the adoption of a ley system of farming in which susceptible pastures (e.g. those with subterranean clover predominant) form a 3- or 4-yr course in a rotation involving ploughing and cropping. Grazing management practices might be so modified as to reduce the attractiveness of pastures to ovipositing beetles.

I. INTRODUCTION

The larva of *Aphodius howitti* Hope has been recognized as a pest of sown and improved pastures in south-eastern Australia for some 25 years. The species is endemic to this country, and is a member of a closely related species group of which the other members are *A. yorkensis* Blackburn and *A. pseudotasmaniae* Given. The taxonomy of this group has recently been clarified by Given (1950). The biology and control of *howitti* have been discussed by Swan (1934) under the synonymic name *A. tasmaniae* Hope.

The Aphodiinae as a whole are poorly represented in Australia, although, with minor exceptions (e.g. Britton 1931), it is the only country in which species of this subfamily are of recognized economic significance. *A. howitti* and *A. pseudotasmaniae* have found in sown and improved pastures, lawns, and golf links, environments favouring the development of exceptionally high population densities. The increasing importance of the pest over the past quarter century has undoubtedly been related to the trend towards higher stocking rates which have involved extensive pasture improvement. *A. pseudotasmaniae* is found only in Tasmania and has been studied by Martyn (1950).

The achievement of pest status by *howitti* is no doubt partly due to its lack of specialization. Its larvae are able to complete normal development on widely different food materials, ranging from organic matter of vegetable origin, to dung or to living plant tissues, alone or in combination. Of probable significance also is the fact that the adult female lays a large proportion of her eggs without a prior maturation feed.

The Aphodiinae are probably primitively coprophagous insects, other feeding habits having been developed as specializations (Schmidt 1935). This author regards the adults of the subfamily as more flexible in their feeding requirements than the larvae, but this is not true of *howitti*. The adults of this species are obligate coprophages, although not, as are many exotic species, restricted to the dung of a particular animal. The exotic species of *Aphodius* are mostly of a smaller size than *howitti*, have much shorter life-cycles (9-10 weeks), overlapping generations, and stages of true hibernation. Whereas these species lay their eggs either singly or in groups of two or three, *howitti* lays large single batches, probably a primitive character.

As the abundance of the species fluctuates greatly from year to year, the interest of graziers in its control tends to be spasmodic; any control measures suggested must therefore be cheap and involve a minimum of interference with the normal routine of pasture management, if they are to be generally accepted.

Control measures for use in bowling-greens and lawns were suggested by Kent-Hughes (1932). The first important study of the biology of the species was that of Swan (1934), who gave an account of the problem in

South Australia. The situation in that State was reviewed by Andrewartha (1945). Cumpston (1941) discussed the biology of the insect and provided a bibliography. The status of the pest in Tasmania has been described by Evans (1941), in Victoria by Twentyman and Pescott (1942), and in the Orange district of New South Wales by Lloyd (1949).

The very marked susceptibility of the young larvae to DDT was demonstrated by the present author (Carne 1948), leading to the recommendation of DDT-impregnated superphosphate for use in the top-dressing of susceptible pastures (Carne 1951). Erlich (1954) has shown that lindane is more effective than DDT or an equivalent quantity of benzene-hexachloride (BHC) and that effective control can be achieved at low cost of materials.

The purpose of the present paper is to describe a general study of the species, its life-cycle, behaviour, food, and oviposition site preferences, and to consider the factors influencing its abundance.

II. GENERAL DESCRIPTION OF PROCEDURES USED IN THE STUDY

(a) Sampling of Populations

(i) *Eggs*.—The eggs are approximately 1 mm in length, and have extremely delicate chorionic membranes; they are laid in batches of from 10 to 60 in cells excavated several inches below the pasture surface. Their small size and fragility prevent the eggs from being separated from the soil by mechanical sieving devices. The most suitable technique for their recovery would undoubtedly be the soil-washing technique of Ladell (1936), but unfortunately the necessary equipment was unobtainable at the time that sampling was carried out.

Two methods were used for the estimation of egg numbers in pastures. In the first, an area (ranging from 1 to 4 sq. lk) was defined and a trench cut surrounding it. The isolated block of soil was then carefully pared away on one vertical face, using a long-bladed knife. The cells were exposed in cross section and the eggs transferred to collecting tubes with a fine camel-hair brush. In the second method, soil samples were taken with a 4-in. diameter Patterson core borer, packed in tins, and taken to the laboratory where they were broken up and the eggs removed.

Both methods have their defects. The former is the more accurate if great care is taken to avoid the crushing or scattering of eggs. The latter, while often more convenient, suffers the disadvantage that the central spike of the boring tool damages eggs lying in its path.

(ii) *Larvae, Pupae, and Immature Adults*.—The density of *Aphodius* populations during these stages was estimated by sieving soil samples in the field, using a mechanical sieving device already described (Carne 1948). The two sieves used had mesh apertures of $\frac{1}{4}$ and $\frac{1}{8}$ in. respectively. There was a certain loss of the smaller larvae through the finer sieve, but

sieves of smaller aperture could not be substituted as these would only pass a very small proportion of the soil. It was found that, by passing the soil through the machine three times when first instar larvae were present, and twice when second instar larvae were present, the loss of these stages did not exceed 3 per cent.

Various sizes of soil sample were tried and that finally chosen was a square block of side 1 lk, dug to the maximum depth at which the larvae were found, which was rarely more than 6 in.

Detailed studies of larval distribution were made by the trenching and paring method, as described for the egg stage. The larvae of *Aphodius*, unlike those of most other scarabaeids, do not move horizontally in the soil. Instead, they construct vertical burrows, from which they emerge at night and move freely over the pasture surface. It was possible to study the distribution of burrows without disturbing the larvae by using plastic knitting-needles to locate the burrow entrances below the loose excavated soil that usually conceals them. Larvae moving on the surface were trapped in V-shaped metal troughs sunk into the soil. Such traps caught large numbers of larvae, but their use involved severe disturbance to the pasture. The troughs used were 8 ft in length, and had a 45° basal angle.

(iii) *Adults.*—On summer evenings, especially in January and February, the beetles leave the ground at dusk and flights may continue for several hours each night. Attempts were made to obtain regular samples of the flying insects by means of revolving nets and sticky surface traps. Such methods proved unsatisfactory, for the beetles readily avoid obstacles when in flight. However, some $\frac{1}{2}$ hr after flights begin, the beetles suddenly develop a strong phototactic response, and use was made of this to obtain a daily index of flight activity.

Light traps of various designs were tried, the most successful were those which employed a mercury vapour discharge tube as an attractant. Traps of the type illustrated in Figure 1 were used to obtain data for the flight-activity studies reported in this paper. The plastic cone about the light source not only serves to protect that element from accidental damage, but actually increases the efficiency of the trap. In its absence, many beetles fly past the light without collision and settle on the ground, rarely taking to flight again.

Light-trap catches do not represent truly random samples of the adult population, for beetles pass through stages when the phototactic response is partially inhibited. Moreover, as in most nocturnal Scarabaeidae, the response is more strongly developed in the male sex. Again, under certain weather conditions, flight may have almost ceased before the response is established. Despite these deficiencies, the consistent fluctuation in catches of several traps operated simultaneously in the same locality (Fig. 2), and the relationship between catch and weather

conditions, suggest that the data obtained does reflect fairly accurately the real fluctuations in nightly activity of the population. Comparison of the total catches over whole seasons provides a reasonably accurate estimate of the relative annual abundance of the species.
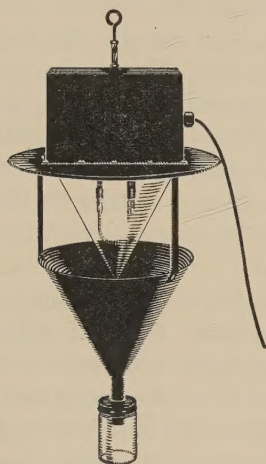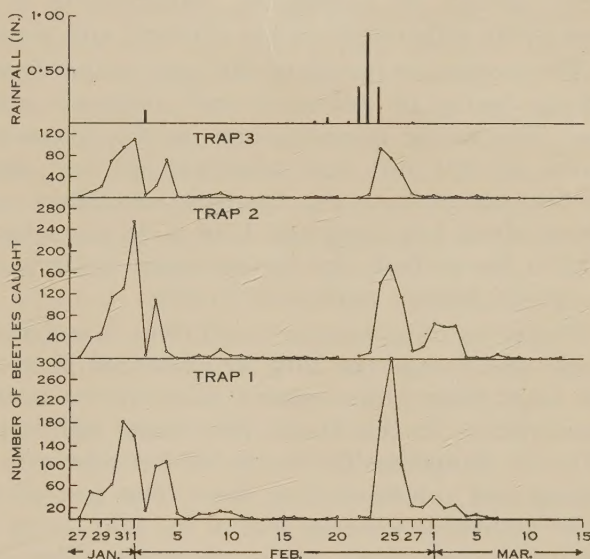
Fig. 1   Fig. 2

Fig. 1.—Light trap used in studies on the flight activity of adults. It consists of a mercury vapour discharge tube as the light source, driven by a high tension transformer operating from the mains supply. The light is surrounded by a cone of transparent plastic. Beetles colliding with this cone fall into the metal funnel suspended beneath and pass into a collecting jar at the bottom. The screw-top lid is soldered to the stem of the funnel. The collecting jar has a ¾-in. layer of plaster of paris which absorbs sufficient tetrachloroethane (the killing agent) to last for 24 hr. The walls of the jar are lined internally with blotting-paper to absorb condensed moisture.

Fig. 2.—Comparison of the nightly catches in three light traps at Black Mountain, A.C.T., in relation to rainfall, for the period January 27–March 13, 1951. Note the general correspondence of the fluctuations of catch between traps and the association of large catches with recent rain.

III. GENERAL BIOLOGY

(a) Seasonal Cycle

Adults appear in flight approximately 15 min after sunset on warm humid nights in summer, most flights being recorded in January and February. Some beetles are attracted towards freshly dropped dung, while others seek out suitable sites for oviposition or may be attracted to lights. Copulation takes place both in the vicinity of dung pads and in or on the soil before flights begin. Those adults that are ready to oviposit burrow down into the soil to a depth of from 2 to 6 in. and make small

smooth-walled cells in which the eggs are laid. After oviposition the adults fly to dung pads where they feed. A second, smaller batch of eggs is developed and these are laid either in the soil beneath the pad or the females may fly off and select an oviposition site elsewhere. The two distinct periods of oviposition, separated by a period of feeding, are subsequently referred to as the primary and secondary ovipositions.

The incubation period of the eggs ranges from 5-14 days in the field; hatching begins in February and continues until mid March in most years. The young larvae remain in the oviposition cell until the head capsule, at first soft and colourless, is fully hardened and pigmented. They then tunnel their way towards the surface and make small individual burrows about 1 in. deep and 1/16 in. in diameter. In the course of their ascent to the surface, the larvae ingest soil and apparently subsist upon the organic matter contained therein.

Under certain weather conditions the larvae leave their burrows at night and forage for dung or preferred plant species. By mid March, when adult flights have ceased, most of the larvae have moulted to the second instar. In this stage, they make burrows 2-3 in. deep and about 3/16 in. in diameter. The larvae do not return to their old burrows after foraging, but construct new ones. The cast of the second instar larva is quite noticeable whereas that of the first instar easily escapes detection. Moulting to the third and final instar takes place from early April onwards, the burrows then ranging from 4 to 8 in. in depth and are approximately 5/16 in. in diameter. A heavily infested pasture is shown in Plate 1, Figure 1, illustrating the large quantities of soil excavated by the third instar larvae. In Plate 1, Figure 2, the overlying soil has been removed from portion of another heavily infested pasture and the burrows clearly revealed.

Foraging occurs at irregular intervals throughout the winter months until September, when the bulk of the larval population is fully fed. The larvae then remain quiescent in their burrows and enter a state of diapause. A short prepupal stage follows in late November, followed by pupation in early December. The onset of diapause is associated with the laying down of extensive subdermal fat deposits and the evacuation of the gut contents. Whereas actively feeding larvae are bluish grey in colour, diapausing larvae are a pale cream-yellow. The evacuated gut material is used to seal off the burrow to form what is later recognized as the pupal cell. The diapausing larvae are capable of active movement if disturbed. In the prepupal stage proper (the term is often loosely employed to include the diapausing stage but is here used in the more restricted sense of Hayes (1929)) the legs are drawn up and non-functional, while traces of pupal structures are visible through the larval cuticle. Transformation to the adult stage begins in mid December and continues through until early January. The young adults remain in the pupal cells until completely hardened and sexually mature.

(b) The Adult Stage

(i) *Behaviour.*—Just before flight begins, beetles may be seen close to the surface of dung pads or in fissures in the soil. Individuals make occasional spasmodic movements, open their elytra, and spread their wings momentarily. Then, as if at a signal, they emerge *en masse* and within a few minutes the pads and the surrounding pasture are alive with seething masses of beetles. Aggregations seen are usually of beetles leaving pads where densities as high as 50,000 per sq. yd may be recorded; very occasionally, beetles emerging from the soil form loose aggregations on the surface before taking to flight. If erect vegetation is present the beetles climb to the tops of blades of grass or old flower stalks. The habit of climbing such vertical supports prior to flight seems to be common to all Aphodiinae. It has been described by Martyn (1950) for *A. pseudotasmaniae* and by Schmidt (1935) for certain Palaearctic species of *Aphodius* and related genera. While this pre-flight activity is in progress, males commonly mount females and perform characteristic pre-copulatory movements in which the antennae are brought into juxtaposition with those of the female and the hind tarsal claws used in genital stimulation. Copulation itself is not observed at this time. The flying population consists of individuals in two distinct physiological states:

(1) Unfed, or partly-fed individuals which are attracted to dung and mostly cease flying before dark.

(2) Fully-fed gravid females searching for oviposition sites, which fly for a longer period and constitute the bulk of the female population attracted to lights.

Under calm conditions, the flight of an individual approximates to a slowly ascending and widening spiral, interrupted by sudden changes of altitude and by short horizontal flights. The insect then flies rapidly and almost directly to another point, perhaps several hundred feet distant, there resuming the special pattern of flight. It will pass within a few feet of a pad without reaction; it is not until a slight breeze develops that the insect is attracted to dung. Flight of many of the beetles (those in stage (1)) then becomes oriented upwind towards the pads, the degree of orientation increasing, and the height of flight decreasing, as the wind velocity increases to a value of 8-9 m.p.h. Any increase of wind velocity above 9-10 m.p.h. results in a complete cessation of flight activity. At velocities from 4 to 6 m.p.h. the approaching swarms can be seen flying upwind as far as 300 ft from a pad. Within 20-30 ft of it, the swarms become recognizable entities, distinguishable from other swarms converging upon nearby pads. The beetles alight on or near the pads and burrow in immediately. Copulation is then frequent and feeding begins. Within 30 min of the time of flight initiation, flight to dung has almost ceased; the remainder of the flying insects consists largely of those in stage (2).

Beetles in pads feed throughout the night and the following day. By the next evening, if large numbers were present, the pads are spread out and flattened, their moisture content so reduced that they are

TABLE 1

PERIODS OF FLIGHT ACTIVITY BY ADULTS OF APHODIUS IN DIFFERENT CENTRES IN NEW SOUTH WALES: A SUMMARY OF 350 COMPLETED QUESTIONNAIRES RETURNED BY GRAZIERS IN 1947-48

District	Locality	Late Dec.	Early Jan.	Mid Jan.	Late Jan.	Early Feb.	Mid Feb.	Late Feb.	Early Mar.
Central western slopes	Rylstone							*	*
	Rylstone						*	*	
	Wellington					*			
	Molong					*	*	*	
	Greenthorpe							*	
	Woodstock					*	*	*	
	Koorawatha			*	*	*	*		
	Frogmore			*	*	*	*		
	Cowra						*		
	Boorowa						*		
	Mudgee						*		
Central Tablelands	Orange					*	*	*	
	Millthorpe						*	*	
	Bathurst					*	*		
	Ben Bullen				*	*	*	*	
	Hampton					*	*	*	
	Carcoar					*	*	*	
	Trunkey						*		
	Taralga						*	*	
	Exeter	*	*	*					
South western slopes	Holbrook						*	*	
	Walbundrie						*	*	
Southern Tablelands	Tumbarumba					*	*	*	
	Yass						*		
	Gunning		*	*	*	*	*	*	
	Crookwell						*	*	
	Bungendore		*	*	*	*	*		
	Bungonia							*	
	Goulburn						*	*	
	Breadalbane							*	*
	Collector			*	*	*	*	*	
	Cooma				*	*			
	Canberra			*	*	*	*	*	*
North coast	Dungog						*		

converted to a light, fairly dry frass. If the weather is suitable when the time of flight initiation is reached, the adults fly off to seek freshly dropped dung. Emergence from pads containing only a few beetles is

relatively slight, consisting only of individuals that have completed feeding. After some days spent in feeding, the females enter stage (2).

Females in this stage, having alighted after flight, walk over the surface, but show no interest in nearby dung pads. Their movements are obviously exploratory; they are halted by plants, small crevices, pebbles, or dung pellets. In the particular pastures where these observations were made, the most frequent mechanical obstructions were small seedlings of subterranean clover. Encounters with these induced a series of exploratory thrusts with the head, the broad clypeus acting as a shovel, assisted by the excavating movements of the sharply toothed fore tibiae. Sometimes at the first such encounter, more often after several, the female selected a point for entry into the soil. It seems to be essential for her to have some firm object against which to obtain leverage in the initial stages of burrowing. The depth to which the insect penetrates is influenced by soil texture and moisture. Under wet conditions it may burrow only to a depth of 1-$1\frac{1}{2}$ in. Several days usually elapse before oviposition begins; if the soil dries out in this time, the beetle extends its burrow to 3 or 4 in. in depth. Most oviposition cells are found at this latter depth, although a few are found within the top inch.

The burrow tends to slope somewhat away from the vertical and is surmounted by a small pile of cast soil. The latter enables entrance holes to be distinguished from emergence holes which are free of cast. At the base of the burrow, the female makes a small cell roughly at right angles to the burrow axis. The insect then reverses its position, widening the cell to form an oval chamber. The eggs are then laid in a cohering mass, after which the insect leaves the cell, plugging the original entrance in a manner which has not been observed. No trace of either entry or departure can subsequently be found immediately adjacent to the cell. The adult returns to the soil surface and may die there, or flies again to dung.

(ii) *Flight Season.*—Light traps have been operated at Black Mountain, A.C.T., since the summer of 1947-48. The dates of first and last appearance of *Aphodius* in the catches, and the total number caught per season were as follows:

1946-47	Jan. 22-Mar. 7	Data incomplete
1947-48	Jan. 14-Mar. 3	Data incomplete
1948-49	Jan. 6-Mar. 10	Data incomplete
1949-50	Dec. 28-Mar. 14	5748
1950-51	Jan. 3-Mar. 8	2920
1951-52	Jan. 11-Mar. 31	5066
1952-53	Dec. 24-Apr. 16	2174
1953-54	Jan. 9-Feb. 25	8245

Questionnaires were sent to graziers in many parts of New South Wales where the species occurs, on which the recipients were asked to record the dates of noticeable flights. A summary of these returns is

presented in Table 1, from which it will be seen that the flight season of *Aphodius* is much the same in all parts of its range in New South Wales. The apparently longer flight period in some districts than others is due, at least in some instances, to certain individuals being better observers than others. From personal observations the author knows, for example, that big flights occurred in Goulburn in late January and early February. The records for Exeter, confirmed by specimens, indicate that flights actually occurred there earlier than at other centres. Exeter
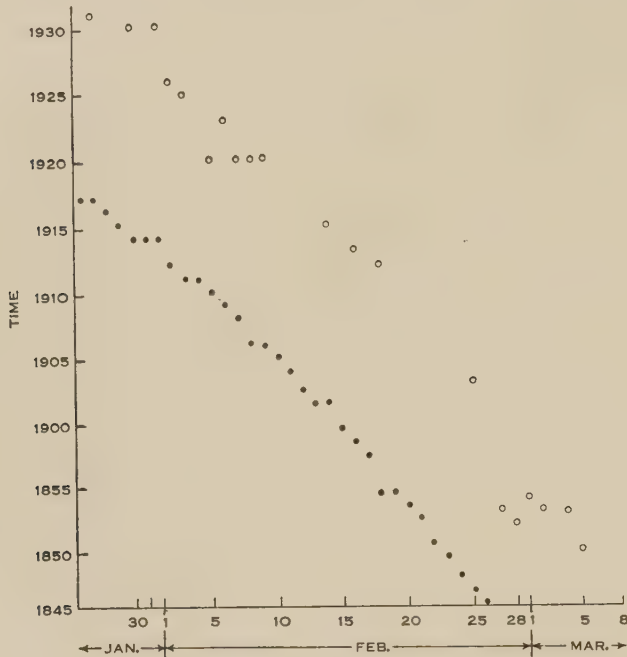
Fig. 3.—The relationship between sunset time and the observed time of flight initiation at Dickson Station, A.C.T., in 1949. Sunset times (●) were calculated from appropriate Air Almanac tables; flight initiation times (○) were recorded in the field.

is very close to the coastwards limit of the species and its earlier appearance there may be due to the influence of the milder coastal climate.

Although very small numbers of *Aphodius* have been taken in ultra-violet light traps in Canberra as late as mid April, flight activity, noticeable to the casual observer, ceases by the middle of March. Such flight records as have been obtained from other States, with one exception, lie within the limits of early January to mid March. The exception is a record from Warrichie on Eyre's Peninsula on April 6, 1948 (information and specimens from the Waite Agricultural Research Institute). The

locality is not one where *Aphodius* would be expected to occur, being situated in a region of very low rainfall. The locality and the date taken together suggest that the specimens might represent a subspecies of *howitti* but no morphological differences can be discerned.
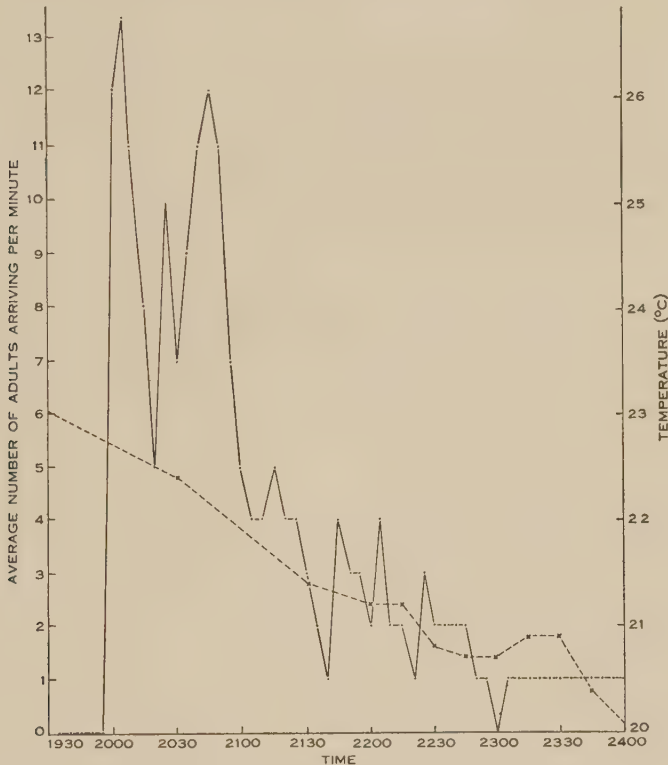
Fig. 4.—The rate of arrival of adults at a light source, in the course of a single evening. Beetles were collected at 5-min intervals and the average number arriving per minute (solid line) and the air temperature (broken line) are here plotted against time. Note the very abrupt onset of the phototactic response just before 2000 hr.

(iii) *Factors Influencing Flight Initiation and Flight Activity.*—As flights begin progressively earlier each evening as the flight season progresses, it seems probable that flight initiation is a response either to light of a certain intensity, or to light intensity decreasing over a certain critical range. In the summer of 1948-49 the time of flight initiation was recorded each evening at Dickson Experiment Station, A.C.T. In Figure 3 the results are shown, together with the curve of calculated sunset time for Canberra. The two curves are highly correlated ($r = 0.97$ for 18 occasions, highly significant at the 1 per cent. level). Slight deviations from the curve of emergence time can be accounted for in terms of local weather, e.g. variations in cloud cover. It was found that flights

TABLE 2

SUMMARY OF OBSERVATIONS ON APHODIUS FLIGHTS AT DICKSON STATION, A.C.T., FEBRUARY–MARCH, 1948

Visual Rating of Intensity of Flight	Date of Flight	A Temperature at Time of Commencement of Flight (°F)	B Relative Humidity at Time of Commencement of Flight (%)	C Temperature at Time of Cessation of Flight (°F)	Prevailing Wind Velocities (ft/min)	Remarks
Very heavy to heavy	2.ii.48	70	72	64	60-90	Flight random
	5.ii.48	66	—	60	0-190	Flight occasionally directional
	7.ii.48	65	64	62	80-300	Flight mostly directional
	9.ii.48	67	54	63	c. 140	Flight mostly directional
	27.ii.48	67	56	64	c. 350	Flight strongly directional
	28.ii.48	67	83	59	20-30	Flight completely random
	4.iii.48	73	—	70	400-600	Flight strongly directional
	5.iii.48	72	—	70	200-400	Flight strongly directional
Moderate	1.ii.48	62	70	61	90-130	Note low temperature at A
	3.ii.48	68	51	54	0-50	Flight not directional, and of short duration due to steep drop in temperature
	14.ii.48	64	29	59	220-240	Soil very dry
	16.ii.48	65	25	57	0-220	Soil very dry
Slight	8.ii.48	72	60	—	320-700	Flight began well but did not develop on account of wind
	18.ii.48	70	22	67	500-550	Combination of dry conditions and fairly strong wind
	19.ii.48	63	70	61	450-850	Combination of low temperature and strong wind
None	21.ii.48	55*	73	—	Extremely variable	Cold, overcast
	25.ii.48	58*	65	54*	200-250	Cold, overcast
	1.iii.48	70*	70	66*	500-1000	Conditions for flight excellent except for very strong wind

* Temperatures taken at times at which flight would have begun and ceased if such had occurred.

always began when the light intensity decreased over the range of 5-2 ft-lamberts. As the light intensity decreases very rapidly at this time of day it was difficult to take accurate readings. The mean value for five occasions was 3.5 ft-lamberts.

Aphodius adults appear to possess what might be termed a "physiological clock" in that attempts to induce flight by artificial reduction of light intensity were only successful at times close to that at which flight initiation would have occurred in the field. This suggests that it may not be light, but some correlated factor, which triggers flight activity. However, although air and soil temperatures are usually falling and relative humidity rising at dusk, these factors may, on occasions, be stable over the relevant period, their gradients may differ greatly from one night to another or may even be reversed, without the slightest effect on the time of flight initiation. To investigate the matter more thoroughly it would be desirable to experiment with larvae reared in a dark-room to preclude the possibility of their being preconditioned to the natural cycle of light intensity. The whole matter is one of considerable interest and it is worth noting that one can, for any evening of the flight season, forecast the time of flight initiation with an error of only a few minutes.

The arrival of adults at a light source in the course of a single evening is characterized by the very abrupt onset of phototaxis. A typical set of data are illustrated in Figure 4. It is usual for more than half the catch of an evening to be taken in the first hour of trapping. In this instance, the cumulative percentages of the total catch at 30-min intervals were 30, 60, 75, 82, 90, 93, 96, 100 per cent.

Although the appropriate stimulus for flight initiation is provided each evening of the flight season, flights do not always occur. Table 2 summarizes observations made at Dickson Experiment Station during the 1947-48 season. Temperature, relative humidity, and wind velocity measurements were made as the beetles left the ground to fly towards dung. Temperatures were again taken when all flight ceased and the wind velocity was measured at 15-min intervals throughout the period of flight.

The data indicate that relative humidity does not influence flight activity but that air temperatures in excess of 60°F are associated with conspicuous flight activity, and that wind velocity plays a limiting role. At velocities of the order of 600 ft/min flight ceases. Under calm conditions, flight is more or less random in direction, but with increase of velocity between 100 and 600 ft/min it becomes increasingly orientated towards dung pads.

More accurate estimates of flight activity than the visual ratings are provided by the light-trap catches at Black Mountain, summarized in Figures 5(a)-5(e). In these, the trap catches for the five seasons 1949-50 to 1953-54 are shown in relation to rainfall and temperature
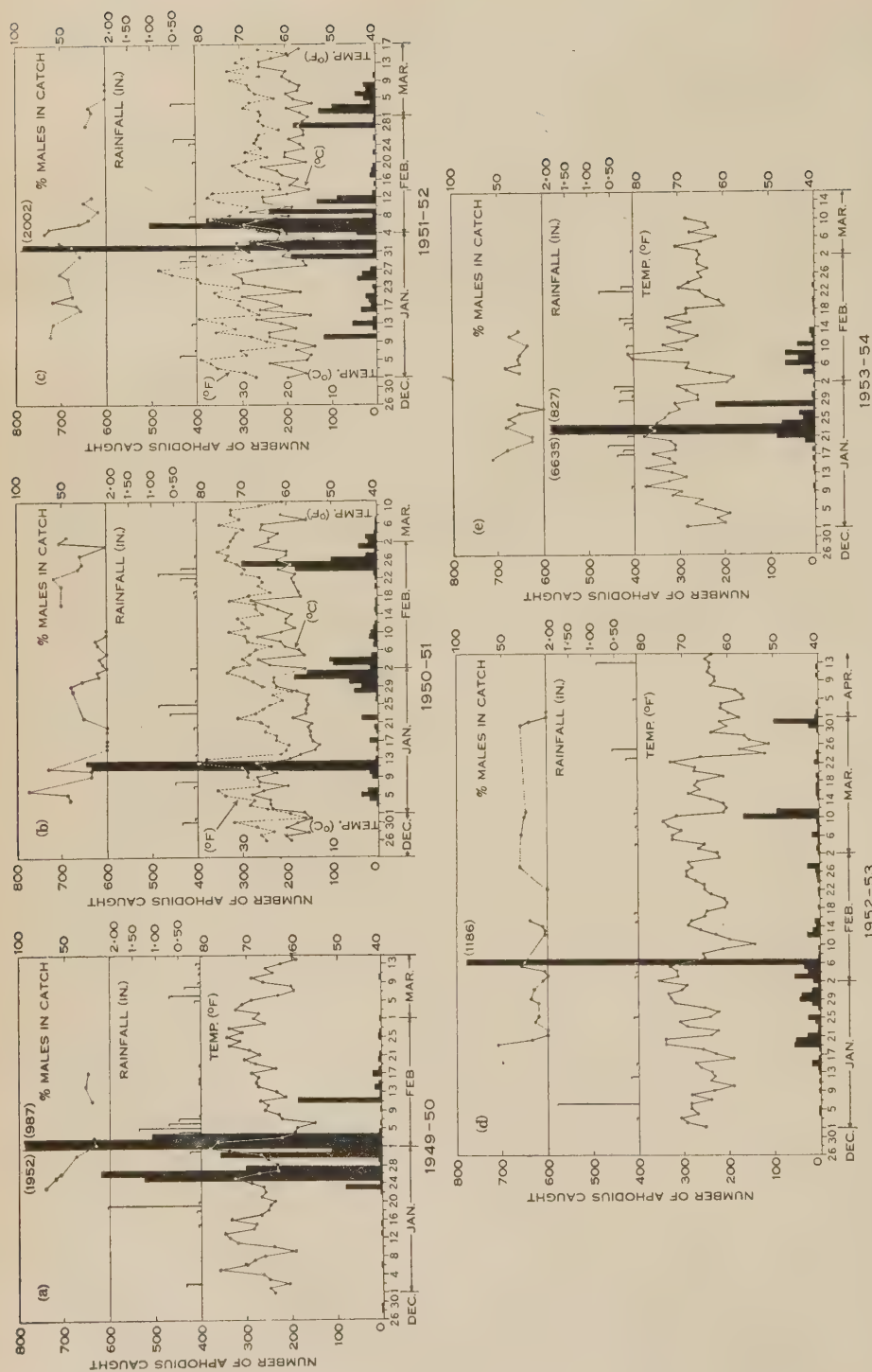
Fig. 5.—(a)-(e) The nightly catches of a light trap at Black Mountain, A.C.T., over the flight seasons of the years 1949-54, in relation to meteorological factors. Beetle numbers are indicated by solid columns, rainfall by vertical lines, daily mean temperatures (°F) and temperatures at the time of flight initiations (°C) by solid or broken lines as indicated in the figures. The percentage of males in the catches are plotted at the top of each diagram. Where the numbers of beetles taken were too large to be shown to scale, the columns are broken and the actual total shown in brackets.

data. In all five diagrams the daily mean temperature is plotted; in Figures 5(b) and 5(c) the temperature at the time of flight initiation is added. A close study of these diagrams suggests that the fluctuation of catch (and, by inference, of actual flight activity) can be interpreted in terms of temperature and rainfall, major flights being associated with recent rain and high temperatures. Fluctuations were more closely associated with temperatures at the time of flight initiation than with daily mean temperatures. Soil temperatures at a depth of 3 in. were recorded in 1950-51 but examination of these records showed that air temperatures were of greater significance in determining the level of flight activity. In the same season, relative humidities were also noted when flights began. Large flights occurred at relative humidities ranging from 10-90 per cent. although most were associated with fairly high humidities.

The coefficient of correlation between catch and temperature at the time of flight initiation for a median 50-day period* of this season was determined as 0.69, significant at the 1 per cent. level.

The unimportance of relative humidity, suggested by field observations at Dickson Station, finds support in these data. The correlation coefficient between catch and relative humidity for the same 50-day period was found to be non-significant ($r = -0.22$), as was also daily rainfall ($r = -0.10$). Inspection of the data shows quite clearly that peak flights are invariably associated with recent rain. However, there is a time lag involved because of the depression of temperatures to unfavourable levels during rainy periods. As relative humidity does not appear to influence flight activity, it seems highly probable that the important factor is soil moisture. It is of interest to note that if the rainfall data were transposed 2 days, the correlation coefficient, although still non-significant, assumed a value of the expected sign ($r = +0.14$).

It has been shown that wind was a very important factor in controlling flight activity at Dickson Station. The Black Mountain light trap was situated in a very protected situation and beetles were caught at times when no activity was observed at Dickson Station. Nevertheless, catches were depressed by high winds. Data on wind velocity could only be obtained from Fairbairn airport, an exposed situation similar to Dickson Station. The correlation coefficient between catch at Black Mountain and the mean of the 6 p.m. and 9 p.m. readings at Fairbairn was significant at the 5 per cent. level only ($r = -0.33$).

The author believes that soil moisture, air temperature, and wind velocity are critical factors in determining whether or not flight occurs, and the level of such activity.

* Analysis was limited to the median period of the flight season in an attempt to reduce errors caused by changes of population density with time. The 1951 catches were particularly favourable for analysis as the peak flights were not grouped in the middle of the season.

(iv) *Food Preferences.*—Swan (1934) has noted that the mouthparts of *A. howitti* adults are poorly sclerotized and not adapted to deal with other than semi-liquid food. Their feeding is in fact restricted to freshly dropped dung, or to the moist interior of old dung pads. That dung is consumed was demonstrated by mixing with it dyes such as fluorescein or methylene blue, which are taken up by the gut epithelium of the insect.

The beetles are strongly attracted to horse, cattle, and sheep dung, to a much lesser extent to that of other herbivores, and scarcely at all to that of carnivores. Fresh horse dung is by far the most favoured food. A comparison of the attractiveness of three types were made on two occasions at Dickson Station in February 1949. Equal volumes of each type (dropped within the preceding 12 hr) were spread on trays 2 ft square and placed out in the field at sunset. When flights had ceased, samples were taken from each and the average number of beetles per sample estimated. By this method cattle dung was found to be 26-51 per cent. as attractive as horse dung, sheep dung only 16-18 per cent.

Cattle dung, which tends to be finer textured and moister than horse dung is usually entered from beneath, whereas beetles enter the latter from its upper surface. Sheep dung, being hard and scattered in the form of small pellets, provides little protection for the beetles. When pellets adhere together, the beetles force their way along the interstices.

(v) *Sex Ratio.*—Martyn (1950) has reported that the sex ratio of pupae of *A. pseudotasmaniae* does not differ significantly from unity. Nearly all counts for *A. howitti* made by the author, whether of pupae or adults collected in the field, or of adults reared from larvae in the insectary, showed a predominance of females. The nearest approach to unity in any large sample was recorded for a batch of 150 reared pupae, 60 per cent. of which were females. Such consistent deviation from a normal 1 : 1 sex ratio has not been observed in the many other scarabaeid species reared by the author, although Schmidt (1935) records similar deviations for three species of European *Aphodius*. No correlation was found between sex ratio and population density. As males were often seen to copulate with a series of females in the field, it would seem that if there is a real deficiency of this sex, it is unlikely to affect the survival of the species.

The percentage of males in light-trap catches was found to fluctuate widely. If the data for percentage of males is superimposed on the diagram of trap catches (see Figs. 5(a)-5(e)) it is noticeable that the value of the former tends to be at a maximum at the beginning of each group of flights within the season and that it then decreases rapidly on subsequent nights.

Sampling of the beetles in dung pads shows an interesting change of sex ratio with time. When mass emergence occurs, a small number of beetles, mostly males, remain in or near the pads. One-day-old dung

retains an attractiveness for unfed adults and females arriving at such pads are seized by the waiting males and copulation ensues. Repeated sampling shows a marked rise in the percentage of males with time, as shown in Table 3.

TABLE 3

THE INCREASE IN TIME OF THE PROPORTION OF MALES IN APHODIUS POPULATIONS FEEDING IN DUNG PADS

Time	Percentage of Males	
	Pad A	Pad B
After invasion	1.6	1.6
24 hr later	5.9	5.4
48 hr later	22.2	17.8

(vi) *Reproduction and Dispersal.*—The earlier literature on *A. howitti* either states or implies that oviposition occurs only once and that feeding on dung is a necessary pre-requisite. Also, that it is the presence of dung that makes a pasture favourable as an oviposition site. This hypothesis is incompatible with several observations made by the author.

Firstly, all nearly mature adult females in the soil have conspicuous ovaries; yet early in the flight season almost all the females captured are without eggs. Thus there is a strong suggestion that a batch of eggs is laid before the insects take part in flights.

Secondly, severe infestations are frequently reported from areas of ungrazed turf where there is no dung present for the nutrition of the adult. From this it may be inferred that either the species can complete its life-cycle in the absence of food for the adult, or that the presence of such food is not an important factor in the insect's selection of an oviposition site.

That oviposition does take place on two occasions was demonstrated experimentally. Adults were reared in completely closed containers from third instar larvae collected in the field. The females laid eggs *in situ* in normal numbers; the females were then removed and placed, each with a male, in small individual containers and supplied with fresh horse dung (previously sterilized to destroy the mite population). Dissection of sample females at intervals shows that feeding and ovarian development were in progress. Viable eggs were laid subsequently. Primary oviposition thus took place in cultures where no food was available to the adult. As the surface of the soil in the cultures was not disturbed, copulation must have followed upon lateral burrowing in the soil, presumably by the males. While this was possible in the moist, finely sieved loam used in the tests, it would scarcely be so in the field, except possibly after heavy falls of rain.

Insectary experiments were carried out to determine whether or not primary oviposition would occur *in situ* if the insects were free to leave

the soil. A further series of cultures containing insectary-reared adults were either left open, or closed with conical wire gauze traps. Trapped adults were dissected and the state of their ovaries noted. The soil from both series was searched for eggs and young larvae at the end of the flight season. It was found that, under these artificial conditions, although some of the females oviposited *in situ,* the majority did not.

The importance of primary oviposition in the survival of the species was demonstrated by protecting areas of pasture against secondary oviposition. The site was a heavily infested subterranean clover pasture near Boorowa, N.S.W. Three wire gauze frames, each 3 ft square and 9 in. deep were embedded in the pasture in November 1950, the pasture beneath them being first cleared of all dung. The larval population densities in the covered plots and in adjacent exposed control plots were estimated in June 1951. The mean density per sq. lk was higher in the control plots (35.2) than in the test plots (29.7), but not significantly so.

In the light of the foregoing evidence, it is not surprising that the species is able to maintain itself in areas of ungrazed turf, such as bowling-greens, lawns, and golf links.

The behaviour and physiology of *Aphodius* adults during reproduction is clearly more complex than previous writers have suggested, and may be summarized as follows:

The abdomens of recently transformed adults are distended with fat-body material derived from the pupae; this is gradually depleted as development of the gonads proceeds. When fully matured the male has functional testes and the female well-developed ovaries. Copulation probably takes place either in the soil or on the soil surface, and the female subsequently oviposits, either *in situ,* or elsewhere, following flight. The beetles then fly to dung, where copulation again occurs and both sexes feed. As the female feeds, a second batch of eggs is developed. When these are mature the female ceases to be attracted to dung and instead, searches for an oviposition site. After laying her eggs, she either dies immediately or may once more fly to dung and there live for several weeks, but without producing further eggs. Males usually die on the ground surface or in the pads. If weather conditions remain persistently unfavourable for flight, the gravid females in dung pads will often burrow and oviposit in the soil immediately beneath. Under such conditions, pads become the centres of small foci of infestation; undoubtedly this phenomenon has led to the belief that the presence of dung at the time of flight is a characteristic of the preferred oviposition site. The author's observations indicate that the type and density of the vegetation and the texture and moisture of the soil are the factors of greatest importance in the female's selection of an oviposition site (see Section IV(*b*)(ii)).

While new patches of infestation appear every year, there is a tendency for old patches to persist for several years, their outlines being retained with remarkable exactitude, suggesting that oviposition *in situ*

is a common occurrence. The odds against duplication of these areas being due to their chance selection by flying adults in successive years are extremely high, especially when the pasture is uniform.

When the females have fed and are selecting an oviposition site for their second batch of eggs, they may well choose a previously uninfested area, thus producing new patterns of infestation.
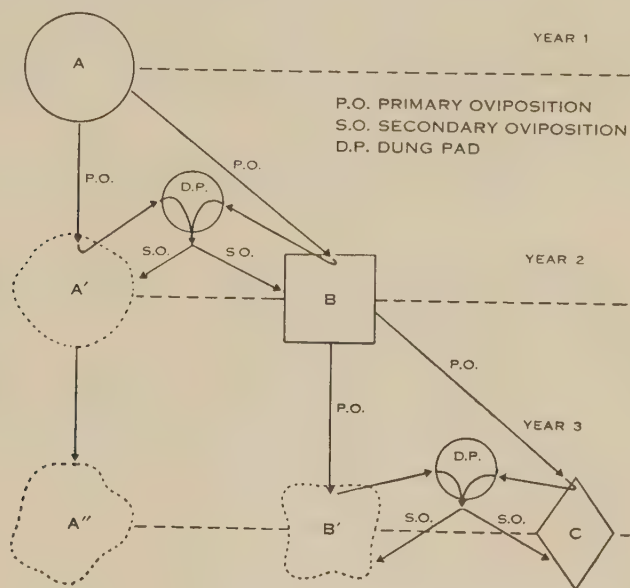
Fig. 6.—Diagram to illustrate an hypothesis accounting for the formation of new, and the duplication of old, patches of infestation. *A*, *A'*, *A''*, and *B*, *B'* represent particular patches of heavy infestation in successive years. Primary oviposition (P.O.) may occur *in situ* (*A-A'*) or elsewhere following flight (*A-B*). The beetles then fly to dung pads (D.P.), feed, and develop further eggs. Secondary oviposition (S.O.) follows on subsequent flight (D.P.-*B*); the site from which the beetle originally emerged may be selected for oviposition (D.P.-*A'*). The process continues the following year, with the formation of a new patch, e.g. *C*. Older patches gradually change shape due to larval migration and eventually disappear.

The process is represented very diagrammatically in Figure 6. The circle *A* represents one of many patches of high population density. Some of the adults emerging from this patch lay their first batch of eggs *in situ*, thus perpetuating it as *A'* in the following year. Other adults fly and select new areas, e.g. *B*, for primary oviposition. They then fly to dung and after feeding and the development of further eggs, proceed to search for an oviposition site. They may (especially in generally unfavourable habitats) select *A'* for secondary oviposition, or, like those adults flying prior to primary oviposition, select some other site, such as *B*. In the following year, *A'* is perpetuated as *A''*, *B* as *B'*, and further new patches (e.g. *C*) are formed. The gradual changes in the outline of the patches

as indicated in the diagram are due to surface movements of the larvae. After several years, re-infestation ceases, probably due to an increase of disease organisms in the soil. Although patchiness is the most outstanding characteristic of populations, it should be appreciated that they are not restricted to these patches; the species is usually found at relatively low densities throughout the whole of any area of favourable pasture.

(vii) *Fecundity*.—Evans (1941) reported that in Tasmania the mean number of eggs per batch was 35. The present author has found the number per batch to decrease towards the end of the flight season, due to the smaller number of eggs laid in the secondary oviposition.

Counts of eggs laid in the primary oviposition ranged from 12 to 56 with a mean of 34.6; for the secondary oviposition, the range was from 4 to 32, with a mean of 15.4. The difference required for significance was 6.1.

The reproductive capacity of the species, expressed as the number of eggs laid per individual, irrespective of sex, is of the order of 25. This value is obtained by assuming a sex ratio of $6:4$ ($♀:♂$) and a 50 per cent. survival of females from primary to secondary oviposition. The factor is then $(0.6 \times 35) + (0.3 \times 15) = 25.5$. This applies to populations in grazed turf, where dung is available as food for the adults; in the absence of dung, the factor has a value of approximately 21.

(c) The Larval Stages

(i) *Factors Initiating the Foraging Activities of Larvae*.—The larvae of *A. howitti* have the unusual habit of emerging at night and moving freely on the surface of the ground under particular conditions of weather. They do not return to their old burrows, but construct new ones adjacent to pieces of dung or certain species of plants.

The association of foraging with rain was demonstrated during the winter of 1949 by trapping larvae in troughs embedded in a moderately infested pasture at Dickson Station. In Table 4 are shown the numbers of larvae caught and the rainfall registrations. All large catches followed rain, the size of the catch decreasing abruptly on succeeding nights. The small catches towards the end of the period resulted from the decrease in foraging activity which occurs at this time of the year, due to cumulative mortality and to cessation of feeding by larvae entering diapause.

Foraging activity only occurs when rain is falling or when the surface of the ground is still wet; it is particularly intense after drought-breaking rain. At dusk, when the light intensity has fallen to approximately the same level as that at which adult flights begin, the larvae emerge on the surface and surface movement, construction of new burrows, and the stocking of these with food ensues. If no further rain falls the surface soil dries out rapidly and foraging activity is much

reduced on the following night, although larvae may climb to the surface and take down such food as they can reach without actually leaving their burrows. Even this activity ceases when the topsoil dries still further and the larvae remain in their burrows where they are capable of surviving for long periods without additional food.

Rain may provide the stimulus for emergence by flooding the burrows and wetting the larvae; however, a very high atmospheric humidity near the pasture surface is necessary if foraging is to take place. Neither high humidity in the absence of rain, nor the watering of pastures when the humidity was low induced this activity.

TABLE 4

RAINFALL AND CATCHES OF LARVAE IN TRAPS AT DICKSON STATION, A.C.T., MARCH–JUNE, 1949

Date on which Either Rain Fell or Larvae Were Trapped		Rainfall (in.)	Larvae Caught	Date on which Either Rain Fell or Larvae Were Trapped		Rainfall (in.)	Larvae Caught
Month	Day			Month	Day		
March	29	0.54	c. 1000	May	25	0.01	—
	30	—	13		29	0.01	—
April	19	0.51	480	June	1	0.01	—
	20	0.14	286		2	0.01	—
	21	0.01	—		3	0.28	10
	29	0.01	—		8	0.13	—
					9	0.03	—
May	3	0.08	—		10	0.01	—
	4	0.54	866		12	0.01	—
	5	0.30	910		14	0.37 ⎫	
	13	0.01	—		15	0.11 ⎪	
	14	0.57	1415		18	0.17 ⎪	
	15	—	47		19	0.04 ⎬ 302	
	19	0.03	11		20	0.01 ⎪	
	20	1.92 ⎫ 2721			21	0.02 ⎪	
	21	0.09 ⎭			22	0.01 ⎭	
	22	—	50				

In another situation, in 1950, troughs were not installed but the piles of cast soil were smoothed down following each occasion of emergence. It was possible to make visual estimates of the amount of surface activity on each occasion. These observations confirmed that foraging is closely associated with falls of rain. It was also found that the proportion of the population emerging is influenced by the distribution of rainy days. Following a prolonged drought, evidence of foraging was very conspicuous but when a series of closely spaced falls occurred, an abruptly decreasing proportion of the larvae responded to these successive stimuli. It is therefore deduced that satiety limits the response of larvae to stimuli for emergence.

The quantity of food taken into new burrows in the 2-3 days following their construction exceeds the current requirements of the larvae; the food material in the average third instar burrow was found to approach exhaustion some 7-10 days later. Field observations indicated that mass emergence only occurs when showers are spaced more than 6-10 days apart.

(ii) *Behaviour during Foraging.*—*Aphodius* larvae, unlike those of other pasture scarabs ("curlgrubs"), are able to straighten out and move quite rapidly on the surface of the ground. Although their progress is necessarily slow among vegetation, they have been observed to move on smooth bare ground at speeds of 10-14 in. per minute. Individuals move randomly until they come in contact with either dung or a favoured species of plant; they do not appear to sense the presence of food until physically in contact with it. Having found suitable food, the larva does not feed immediately but proceeds to excavate a burrow beside it. After penetrating several inches, the larva climbs to the surface head foremost and cuts off pieces of plant leaves, or seizes fragments of dung, and drags these to the bottom of the burrow and presses them against its sides. The process is repeated three or four times in the next hour, after which surface activity gradually ceases. Once the burrow has been constructed, and until the next occasion of mass emergence, the larva never leaves it completely, but always keeps the tip of its abdomen inside the burrow opening. If a larva is moved even a short distance away from its burrow, it is unable to find it and after a short time, begins the construction of another.

For two or three nights after burrow construction, the larvae continue to burrow deeper into the soil and so increase the volume of cast soil on the surface of the pasture.

(iii) *The Mechanics of Burrow Construction.*—Andrewartha (1945) suggested that, in constructing burrows, the larva passes the soil through its gut and extrudes it upon the surface through its anus. While larvae undoubtedly do consume quantities of soil, the volume thrown up in a single night may be many times the entire body volume of the larvae itself. The author has observed burrow construction in the field and found it to be due to excavation.

In the initial stages, plants, pieces of dung, or small crevices in the soil are used as points of leverage. The soil is removed by downward strokes of the head, that loosened being passed backwards between the legs. Once the soil is penetrated, the larva excavates in a downward spiral, so that the diameter of the burrow is considerably greater than that of the larva itself. At intervals, the abdomen is drawn forward and placed beneath the excavated soil which is then raised to the surface by a violent bodily flexure. When large numbers of larvae are making burrows simultaneously, the observer can actually hear the spasmodic eruptions of soil and watch the piles of cast soil increase in size as this occurs.

(iv) *Factors Influencing the Development of Larvae.*—Sampling of larval populations in different sites reveals very considerable differences in their rates of development.

In sheep-grazed subterranean clover pastures on clay-loam soils (characteristic of chronically infested grazing country on the Southern Tablelands of New South Wales) larval development continues throughout the winter; it is not until early spring that the majority of the larvae are fully fed. In more favourable environments, development may be much more rapid and the larvae fully fed by early winter.

Observations made over a period of years suggest that development is influenced both by the type of food accessible to the larvae and by the texture of the soil in which they burrow. From January 1949 to March 1950, regular samplings were made at two sites in Canberra. Site *A* was portion of a sheep-grazed pasture as described above. Beneath the topsoil was a hard clay horizon at a depth of 6-8 in. into which the larvae did not penetrate. Site *B* was portion of a golf links fairway, where various annual grasses, native clovers, medics, and several species of flatweed grew on a deep, very soft alluvial loam. The samples provided information on the duration of each stage of development. This information is summarized diagrammatically in Figure 7, in which each symbol is virtually a distribution curve of each stage in relation to time.

It will be noted that larval development was much more rapid in site *B* where most larvae had entered diapause by the end of May, than in site *A* where this stage was not reached until the end of October. The period of diapause was greatly prolonged in site *B* so that both pupation and oviposition were synchronous in the two sites. These were situated within a few miles of each other and subject to almost identical climatic conditions. The great differences in the growth rates of the larvae cannot therefore be associated with differences in temperature.

The very rapid development of the larvae in site *B* appears to be related to the extremely deep, friable soil there. The author has frequently observed that larvae living in the lighter soils develop more rapidly than those in heavier soils, irrespective of the nature of the vegetation and the presence or absence of dung. It seems reasonable to suppose that the rate of development is influenced by the energy expenditure required in burrow construction.

The influence of different foods on larval growth is less apparent. In experiments to determine the most suitable means of culturing *Aphodius* in the insectary, larvae were kept in containers of a light clay-loam and provided with various kinds of dung and vegetation, alone or in combination. The differences in growth rates were scarcely significant. The best combination proved to be sheep dung placed on top of sub-terranean clover growing in the containers. However, even more rapid growth was recorded in a parallel series of cultures in which no food

was provided on the surface but in which the soil had been previously mixed with 25 per cent. of its volume of composted lawn grass clippings.

It is quite evident that larvae are able to use organic matter in the soil as their sole source of food. Very rapid growth has been noted in lawns, especially where piles of lawn clippings have lain, in the kitchen
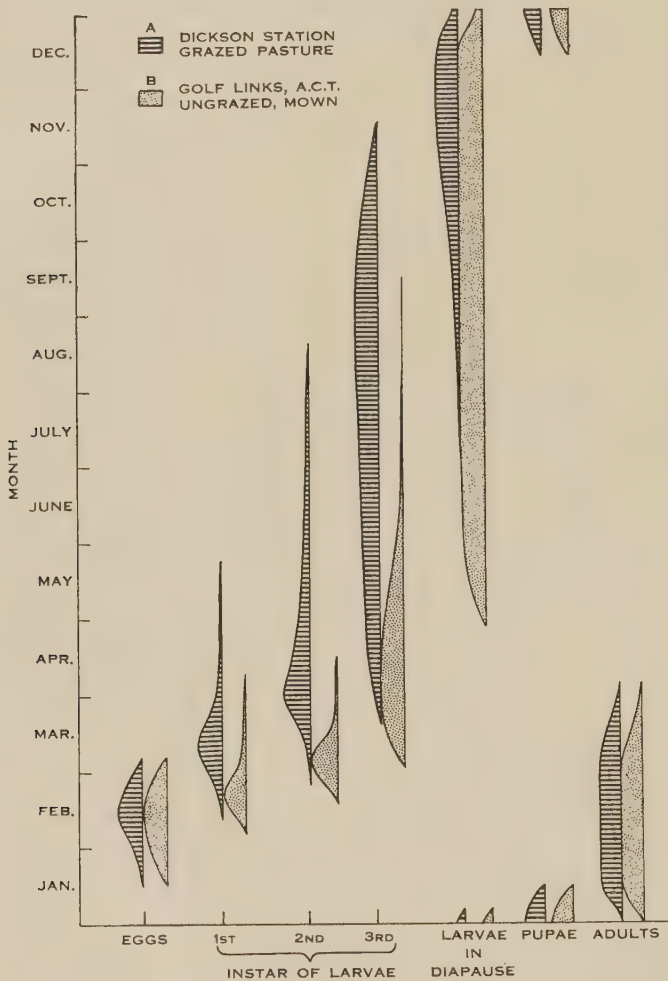
Fig. 7.—Diagrammatic representation of the development of two populations of *Aphodius* larvae in Canberra in 1949. The widths of the columns are proportional to the percentage of the population in the particular stage. Note that, although development was much more rapid in population *B* than in *A*, pupation and oviposition were synchronized by differences in the duration of the diapausing stage.

garden areas of derelict homesteads, and in old, unused stock camps. All such situations are characterized by soil with a high humus content. The larvae from such situations are not only more advanced but actually larger than those from infested pastures generally. It was expected that

their greater size would be reflected in that of the adults produced. Light-trap samples were taken on February 11, 1950 at Dickson Station and in a closely settled locality in Canberra where *Aphodius* infestations had been severe in lawns the previous autumn. In Figure 8 are shown
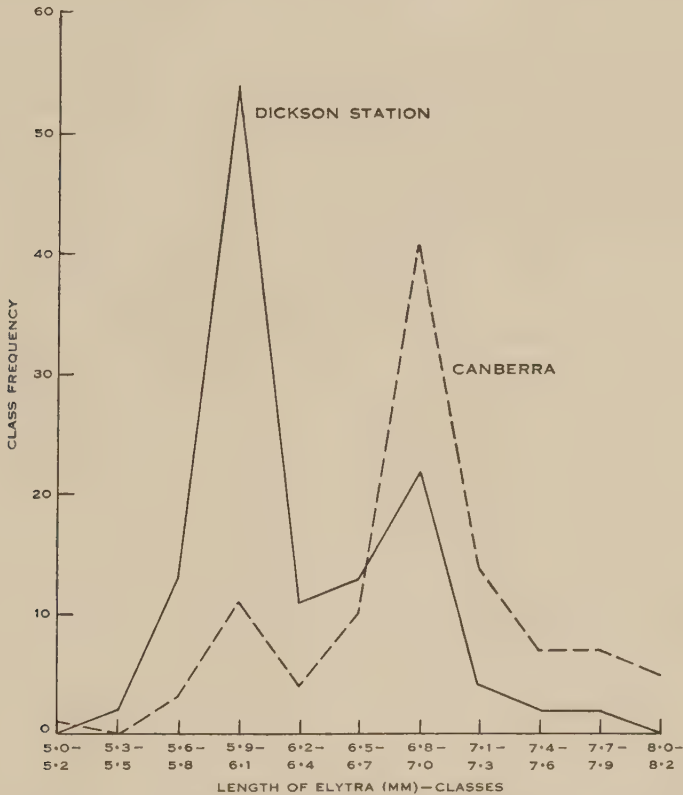
Fig. 8.—The distribution of size classes of males from two localities, showing the greater average size of individuals derived from watered garden soils than of those derived from permanent pastures under natural rainfall in the Canberra district.

the distributions of elytral length classes of the males in these two samples. The Canberra specimens are appreciably larger than those from Dickson Station.

It was observed also that the coloration of individuals was consistently darker in beetles from lawns, than in those from dry-farmed pastures. This may be due to the watering given to lawns, as in other work the author has found that the intensity of pigmentation of scarabaeid adults is influenced by the moistness of the larval environment, the lighter-coloured individuals being obtained when larvae are reared in soil of relatively low moisture content.

IV. Distribution and Numbers

(a) *The Large-scale Distribution of the Species*

Apart from a few anomalous records, the area of distribution of the species may be defined as a broad tract of country extending from the south-east corner of South Australia, across Victoria into the Southern Tablelands of New South Wales. To the south it extends to Tasmania and the islands of Bass Strait. In South Australia and Victoria *Aphodius* is found in suitable habitats from the coast to an inland limit coinciding approximately with the isohyet of 20 in. average annual rainfall. The axis of the distributional area in these States is therefore east-west. This axis is deflected to the north-east in New South Wales, where the inland limit diverges from the 20 in. towards the 25 in. isohyet, especially to the north of Cowra. The northernmost record is from Singleton, N.S.W. Only in the extreme south of New South Wales are infestations found on the coastal plain. The coastwards limit of the species to the north of Nowra corresponds with the eastern edge of the Tablelands. In Tasmania the situation is at present doubtful. No means of distinguishing the larvae of *A. howitti* and *A. pseudotasmaniae* have yet been discovered. As surveys are necessarily based on the larval stage, conclusions on the distribution of the two species cannot be made, although collections of adults seem to point to *howitti* being the dominant species in the northern half of the island (Martyn, private communication).

The author made transects across several parts of the inland limit of the species to the north-west of Canberra in three successive years (1947-49) and was unable to detect any variation in the position of this limit. Surveys were made in the winter months, the soil being examined for larvae every 3-5 miles. The most favourable sites were selected for sampling. While this stability of distribution could be due to the weather or other environmental factors not varying sufficiently over a short period to cause any change, it must be pointed out that the author was unable to discover any record of the species having been found west or north of the limits established by these surveys in New South Wales or Victoria respectively. Although the area of distribution may at times have contracted towards the coast, there is no indication that the species has ever occurred inland of the limits determined in 1947-49.

It was noted that, very close to the margin of its climatic range, the species was just as abundant locally as in the central part of that range. However, the places suitable for occupation were fewer and much smaller in the latter than in the former. This appeared to be the principal reason for the relatively low total numbers observed in the marginal areas.

As the distributional limits of the species do not appear to vary appreciably from year to year, the area enclosed by them can be regarded as having a climate permitting the species to survive in even the most unfavourable years. That *Aphodius* is apparently unable to take

advantage of favourable climatic conditions which must occasionally occur in areas outside these limits is probably due to its long life-cycle and limited flight range. Moreover, the chance of individuals being wind-borne into new areas must be limited greatly by their complete cessation of flight activity when the wind velocity rises above a very moderate figure.

Soil moisture and temperature are those aspects of climate which are probably of greatest importance to the survival of the species. Deficient soil moisture is presumably the factor preventing it from occupying country inland of the 20-in. isohyet. In districts near this limit, larvae were found only in exceptionally wet situations. On the other hand, the level at which rainfall becomes unfavourably high seems to be modified by temperature. For example, an annual rainfall of 40 in. is "excessive" on the coast of New South Wales but in cold subalpine regions (e.g., Kiandra, Adaminaby, and Mt. Kosciusko) *Aphodius* thrives although the rainfall may exceed 60 in.

Although it is a native species, *A. howitti* has not been found in association with the dung of other than introduced mammals, and its natural diet is unknown. Special efforts were made to locate and examine dung of native animals. While wallaby and kangaroo dung were found to contain a rich fauna of other *Aphodius* spp., *howitti* was never represented.

Before the coming of the white man to Australia, the species probably existed, as it does at present in unimproved native pastures, at extremely low levels of population density. Man's activities have undoubtedly allowed it to occupy great areas of country that were previously quite unsuitable to it.

The species has only become a severe pest since pasture improvement began. The distribution of areas of severe damage at first followed quite closely upon the main railway lines (see Swan's 1934 map of the distribution of pasture damage in South Australia). In the early days of pasture improvement, top-dressing with superphosphate was undertaken most frequently on properties lying near to existing railheads, as all fertilizers were brought by train from the cities. *Aphodius* did not build up to high numbers in the areas not served by railways until the extension of road transport services made large-scale pasture improvement feasible there.

In the least-improved country, *Aphodius* is difficult to find except in special situations. For example, in the native pastures in the Snowy Mountains area, it is abundant only in stock camps and stockyards or in their immediate vicinity. In such situations, the composition and physical characteristics of the vegetation have been greatly altered by intense grazing and trampling and subterranean clover often is introduced. Elsewhere in such country, the species exists at very low levels of population density but increases in numbers wherever areas of suitable habitat are developed.

It seems likely that *Aphodius* has penetrated along newly constructed roads into areas never previously occupied by it. In heavily forested country near Omeo in Victoria, and in the Burragorang Valley in New South Wales, search in uncleared areas has never yielded a single specimen, but in small clearings grazed by travelling stock and on roadside verges, larvae were found to be very abundant. Presumably the species migrated along these roads and became established in these very restricted habitats. The larval densities noted were extremely high, suggesting that *Aphodius* might become a serious pest were such country cleared and used for grazing on a large scale.

In districts where greatly increased carrying capacity has resulted from the use of fertilizers and the introduction of subterranean clover, *Aphodius* may cause severe damage to pastures in years of peak abundance.

(b) The Distribution of Populations in Grazing Land

(i) *General Observations on the Types of Pasture Preferred.*— During the course of surveys of the distribution of the species, observations were made of the characteristics of pastures in relation to the presence or absence of *Aphodius*.

The preferred oviposition site may be defined as pasture or sward containing a high proportion of leguminous plants, especially clovers, which is short and does not provide a complete ground cover in summer, growing on a well-drained soil of medium texture. Typical sites are illustrated in Plates 1 and 2. Tall and rank or short and dense vegetation, especially if lacking a leguminous element, is avoided.

Estimates of larval populations were made in 1947-48 in a number of pastures at Dickson Station. Pastures of several types were available for study and some of these had been subdivided, and grazed at different rates over a period of years. The results are summarized in Table 5. Each estimate is based on four 4-lk square samples from each of six randomly distributed sample areas. Pasture No. 1 was a mixed, sown pasture of *Phalaris tuberosa,* lucerne, and subterranean clover. No. 2 consisted of perennial rye grass and clover, the latter predominating. No. 3 was similar to No. 2, but with the grass predominating. All these pastures had been heavily grazed. No. 4 was similar to No. 1 but had never been grazed; 4a was a site on a rise in that pasture, 4b a site in a depression. No. 5 was again similar to No. 1 but had been severely overgrazed. No. 6 was a paddock of reverted crop-land; 6a was typical of the paddock as a whole, 6b of a sheep camp located in it.

The estimates of larval density in these pastures confirm observations that were commonly made by the author in the course of field surveys:

(1) That when grasses are present and form a continuous ground cover in summer and clovers are absent or sparse, infestation is light (cf. Table 5, Nos. 2 and 3);

(2) That the degree of infestation is roughly proportional to the grazing intensity (cf. Table 5, Nos. 4*a*, 2, 5, and 6) ; and

(3) That depressions are infested to a lesser degree than the tops of rises (cf. Table 5, Nos. 4*b* and 4*a*).

Neither lawns nor pastures experience severe infestation until the third or fourth season from the time of planting, possibly due to the disturbed condition of the topsoil. There is some evidence that light initial infestations may cause changes in the composition of a pasture which increase its favourableness as an oviposition site. In improved or sown pastures consisting of subterranean clover and either native or introduced

TABLE 5

POPULATION DENSITIES OF APHODIUS IN A NUMBER OF HABITATS AT DICKSON STATION, A.C.T., IN 1947-48

Estimates based on four 4-lk square samples from each of six randomly distributed sample areas within each pasture

Date	Pasture No.*	Mean Density of Larvae per Sq. Lk
July 1947	1	5.3
	2	22.0
	3	0.1
	4*a*	11.2
	4*b*	1.6
	5	27.5
June 1948	6*a*	0.0
	6*b*	31.0

* See description in text.

grasses, heavy grazing and top-dressing with superphosphate tend to cause the clover to become predominant, so increasing the likelihood of infestation by *Aphodius*. Wherever patches of infestation occur in such pastures, this trend is accelerated.* For example, Plate 1, Figure 3, shows part of a mixed pasture; it will be noted that grasses are almost eliminated where larvae have been exceptionally numerous, contrasting with the grass-predominant pasture nearby. In native pastures that have been harrowed, top-dressed with superphosphate, and sown with subterranean clover, the native grasses are gradually eliminated. The area supporting a dense *Aphodius* population stops short at the junction between improved and unimproved pasture (Plate 1, Fig. 4).

* This occurs despite the preference of larvae for subterranean clover as compared to grasses. When infestation is severe and the vegetation is almost destroyed, the clover re-establishes rapidly from "hard" seed remaining in the soil from previous seasons, whereas annual grasses are only replaced by seed subsequently carried in from less severely damaged pasture. This usually fails to become established as a result of competition from the already well-established clover plants.

Aphodius is found in a wide range of soil types, ranging from sands to light clay-loams. Most infestations were recorded on grey, greyish brown, or reddish brown soils. The species was not found in heavy black or yellow soils. The texture of the soil appears to be of more importance than its chemical nature . Series of soil samples were taken in heavily infested and adjacent uninfested sites in various parts of New South Wales and used for pH and total nitrogen determinations. Neither factor showed the slightest correlation with the presence or absence of *Aphodius*.

(ii) *Detailed Studies on the Small-scale "Patchiness" of Density Distribution.*—A well-known characteristic of all populations of larval Scarabaeidae is their very irregular density distribution. While it may be possible to define broadly those areas of pasture susceptible to severe, moderate, or negligible infestation, detailed forecasts of where larvae will be most numerous in a particular paddock usually prove inaccurate.

Sampling of the soil for eggs was carried out in several seasons at Dickson Station and on a property near Boorowa. Egg distribution was first studied in an undulating site at Dickson Station, the pasture consisting of *Phalaris tuberosa,* subterranean clover, and lucerne. Eggs were found most abundantly in soil on the upper slopes and the tops of rises, only rarely in depressions. The most conspicuous differences between such situations were the taller and denser vegetation in depressions and the higher soil moisture level, especially shortly after rain. Attempts were made to simulate the favoured conditions provided by sheep camps by severe clipping of the pasture and by top-dressing with large quantities of sheep manure. Such plots became heavily infested if laid down in topographically favoured situations; when situated in depressions no infestation resulted, although the beetles visited the plots to feed.

A characteristic example of the relationship of infestation to topography is illustrated in Figure 9. Here an undulating pasture was surveyed and the zones of severe, moderate, and negligible infestation shown in relation to the 6-in. contours.

An almost flat subterranean clover pasture was then examined. Sampling was carried out during the egg stage; these were found to be concentrated markedly in small very shallow depressions, such as that illustrated in Plate 1, Figure 5. The summer had been particularly dry in the year of sampling. The following year, after a much wetter summer, the pasture was again sampled and eggs were found to be equally abundant in level ground as in depressions. It would therefore seem that the distribution of eggs in a pasture is determined, in part at least, by soil moisture differences at the time of oviposition. This might be due to a preference of the females for soil of a particular moisture content, or to an effect of soil moisture on the survival or fecundity of the females.

The distribution of egg batches was observed in relation to individual plants and dung pads. Even in the most homogeneous pasture, the density

distribution of egg batches is very irregular at this scale of observation. Sampling in a pasture consisting solely of subterranean clover showed that the distribution of eggs was highly correlated with that of the plants. Eggs were rarely found in soil devoid of plant cover unless dung happened to have been present at the time when females were searching for ovi-

HEAVY INFESTATION   MODERATE INFESTATION   SLIGHT OR NO INFESTATION

6-IN. CONTOURS
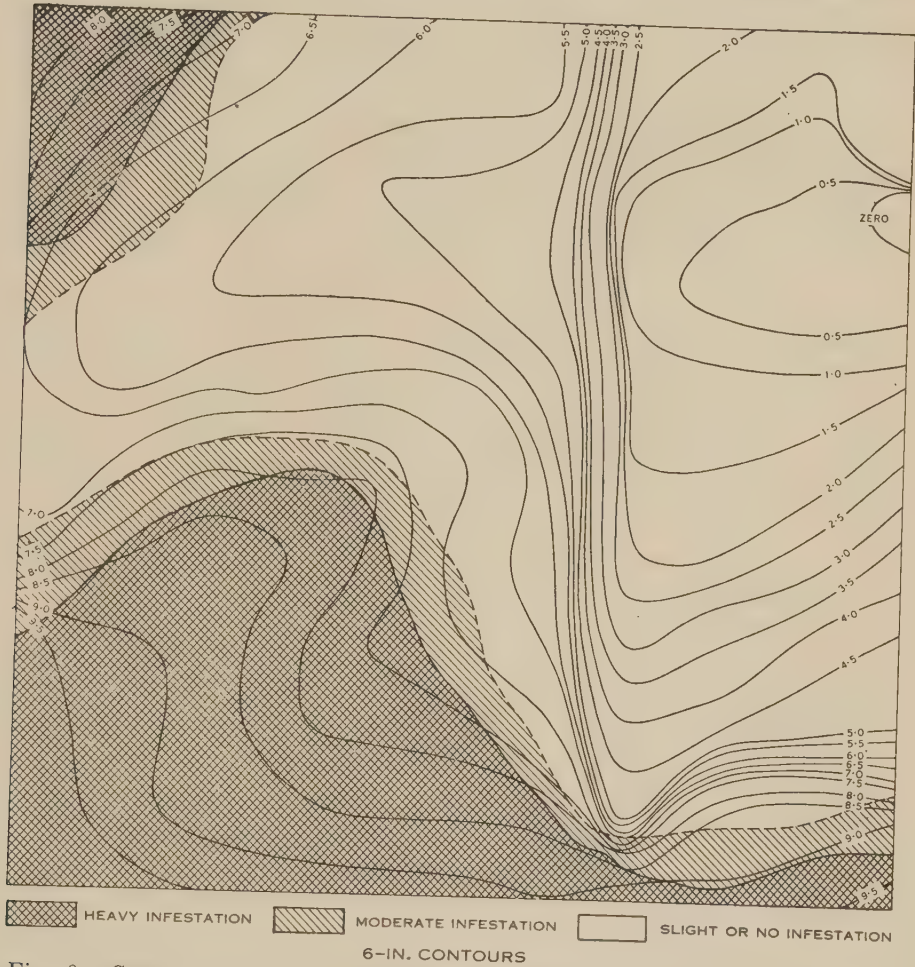
Fig. 9.—Contour map of portion of an undulating sown pasture, showing the relationship between slope and degree of infestation by *Aphodius*.

position sites. For example, seven 4-in. diameter core samples taken in bare ground yielded no eggs; eight samples taken beneath clover yielded 0, 0, 1, 1, 3, 4, 9, and 14 eggs or newly hatched larvae.

In mixed pastures, eggs were found much more frequently adjacent to or beneath legumes (clovers or lucerne) than grasses. Eggs were also sampled in a native *Stipa* pasture that had been improved by the introduction of subterranean clover and the broadcasting of superphosphate.

The vegetation at the time of sampling consisted of a mosaic of clover and grass, the former occupying the space between tussocks of the latter (Plate 1, Fig. 6). Eggs were found only under portions with a clover cover.

As the larval stages feed on living vegetation and prefer legumes to grasses, the observed distribution of eggs would seem to provide for the survival of the species. The author considers that the gravid female is attracted to vegetation, or even dung, not because of the intrinsic food value of these materials either to itself or its young, but merely because entry into the soil is easiest in such situations. The apparent preference for oviposition under clovers rather than grasses may well be due to the breaking up of the soil crust by recently germinated clover seedlings. These provide innumerable points of entry into the soil. On the other hand, the soil beneath perennial grasses tends to be smooth and hard.

TABLE 6

POPULATION DENSITY OF LARVAE IN SUCCESSIVE SQUARE LINK SAMPLES TAKEN AT RIGHT
ANGLES TO AN ADVANCING FRONT

Transect	4 Lk behind Front	3 Lk behind Front	2 Lk behind Front	1 Lk behind Front	On Front	1 Lk beyond Front
A	32	62	68	82	95, 53	14
B	9	15	14	21	65, 100	10
C	15	23	19	13	33, 30, 14	0
D	9	6	16	15	24, 16	0

It is very much simpler to make observations on the distribution of the larval stages, especially the later instars, than on the egg stage, for the soil thrown up during burrow construction allows a ready visual appreciation of the pattern of density distribution.

It was considered important to know whether the patterns of egg and larval distribution are similar, or whether oviposition occurs more or less at random and the patchiness of larval distribution is due to differential mortality or other factors. By sampling pastures in which the studies on egg distribution were made, it was found that the former alternative is correct. There is, of course, a slow change in the distribution of larvae in the course of their active life, for in foraging and constructing new burrows, they tend to move out from areas of high to areas of low population density.

When eggs are laid abundantly in small areas, e.g. the slight depressions referred to above, the subsequent larval density is very high, often exceeding 300 per sq. lk, and the vegetation may be completely destroyed. When larvae are foraging, they do not receive a stimulus for burrow construction unless they find a suitable source of food. Even although their direction of movement appears to be indeterminate, the

net result is that most larvae move into comparatively undamaged vegetation. Very dense accumulations of larvae are found about the peripheries of infested patches of pasture, which enlarge on each occasion of emergence and foraging. The thick piles of cast soil are very conspicuous, and are here referred to as "fronts". Typical fronts are illustrated in Plate 2, Figures 7, 8, and 9.

If a series of samples of the population are taken consecutively along a line at right angles to a front, a characteristic density distribution is observed. Typical data are presented in Table 6. Behind the front, in the area devoid of vegetation, are found the smaller, less active larvae and larvae that have entered diapause and ceased to take part in surface activities. The individuals in the front itself consist of larger, more active specimens. In advance of the front, the larval density is relatively low.

It is not always possible to account for the distribution of these patches of high larval numbers. A great many observations were made, in the expectation that these would enable deductions to be made concerning the major characteristics of the preferred oviposition site.

In very general terms, the most uniform distribution of larvae is found in pastures that are most uniform in vegetation and topography. However, the density distribution of larvae is always uneven and patches of abnormally high numbers are found even in the most uniform environments. Patchiness may be due, as suggested above, to preferential oviposition in soil of an optimum moisture content, or in pasture of a particular vegetation density. Larvae are often exceptionally numerous parallel and adjacent to fences, about trees or tree stumps, or about ornamental shrubs in lawns. One pasture examined was strewn with derelict machinery, stumps, and builder's rubbish, and about each such object was a zone of heavy infestation. An extreme example of this association of high larval densities with outstanding objects was found in a large paddock in which the only conspicuous object was an iron post, some 5 ft high. The paddock carried a fairly uniform improved pasture and contained only one large patch of infestation which was centred exactly on the post.

On hillsides, trees are frequently surrounded by circular or oval patches of infestation. This was at first thought to be associated with the presence of dung dropped by sheep sheltering beneath such trees, but the same phenomenon was observed on ungrazed pastures. These and other observations strongly suggest that the ovipositing females are attracted towards conspicuous objects. Such behaviour is exhibited by many other Scarabaeidae. For example, the melolonthine *Anodontonyx noxius* Arrow (the wheat root scarab) swarms on hot summer afternoons and flies towards fence posts, people, animals, or machinery. In this instance the attraction appears to serve the purpose of bringing the sexes together for copulation, the females returning to cultivated soil to lay

their eggs. Oviposition about tree stumps is characteristic of the cane beetle *Lepidiota caudata* Blackburn (Anon. 1948). Schneider (1952) in a most valuable paper, has described the orientation of the flight of the European cockchafers *Melolontha melolontha* L. and *M. hippocastani* F. towards conspicuous objects on the horizon.

NO. OF LARVAE/SQ. LK IN EACH PLOT

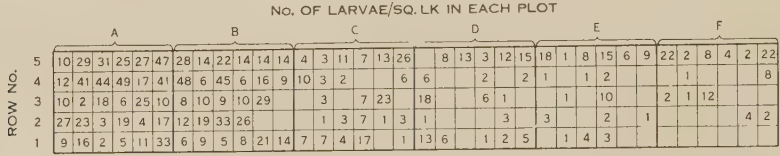|	A						B						C						D						E					F					
5	10	29	31	25	27	47	28	14	22	14	14	14	4	3	11	7	13	26	8	13	3	12	15	18	1	8	15	6	9	22	2	8	4	2	22
4	12	41	44	49	17	41	48	6	45	6	16	9	10	3	2				6	6				2		2	1		1	2			1		8
3	10	2	18	6	25	10	8	10	9	10	29				3		7	23	18			6	1				1	10		2	1	12			
2	27	23	3	19	4	17	12	19	33	26			1	3	7	1	3		1			3		3		2	1			4	2				
1	9	16	2	5	11	33	6	9	5	8	21	14	7	7	4	17		1	13	6		1	2	5	1	4	3								

ROW NO.

Fig. 10.—Diagram of an experimental site at Dickson Station, A.C.T., showing subdivision into blocks and plots (each 20 × 25 lk). In each plot is shown the number of larvae per sq. lk in population sampling carried out in July 1946.

However, infestations are not restricted to situations where conspicuous objects are present. Patches of severe infestation occur in extensive level pastures where no such explanation of their distribution is possible. In some instances, the patches appear to be associated with small areas which differ in some way from the main body of the pasture, often in respect of soil texture or vegetation. Yet there are many instances

TABLE 7

LARVAL DENSITY IN RELATION TO THE PRESENCE OF LUCERNE IN SAMPLES TAKEN FROM A LUCERNE–SUBTERRANEAN CLOVER–PHALARIS TUBEROSA PASTURE AT DICKSON STATION, A.C.T., JULY 1947

The expected frequencies for a distribution not influenced by the presence of lucerne are given in brackets

Presence of Lucerne on Sample Area	No *Aphodius* in Sample	*Aphodius* Present in Sample	Total
Absent	43 (35.4)	65 (72.6)	108*
Present	16 (23.6)	56 (48.4)	72
Totals	59	121	180

* $\chi^2 = 5.296$ $(n = 1)$; $0.02 < P < 0.05$.

where pastures appear quite uniform to the observer and there seems to be no reason why the females should prefer to oviposit in a number of small sites, to the virtual exclusion of the remaining pasture. It was assumed that there must be small differences that made these sites attractive and it was hoped that these might be revealed by closer examination. With this end in view, larval distribution was studied on a smaller scale. The site chosen was a mixed pasture at Dickson Station used by the Plant Industry Division, C.S.I.R.O., for experiments in the response of pasture to a range of lime and superphosphate treatments.

The site (Fig. 10) was divided into six blocks (A to F) each containing 30 plots measuring 20×25 lk. Materials had been applied on a plot basis, the treatments being replicated randomly within each block, except that line treatments were restricted to row 5. In each plot several areas, each 1 lk square, were designated for study. The pasture composition on these sample areas was measured both in terms of species weight and species cover. The pasture was then dug and the larvae collected for sorting and counting and a sample of the soil retained for pH determination. In Figure 10, the number of larvae in a sq. lk sample as at June 1946 are shown for each plot. The trend towards heavier infestation in row 5 suggests a preference for the limed plots but the trend is equally pronounced in the control plots. An avenue of planted eucalypts runs parallel to the experimental area adjacent to row 5 and its presence might account for this gradient in larval density.
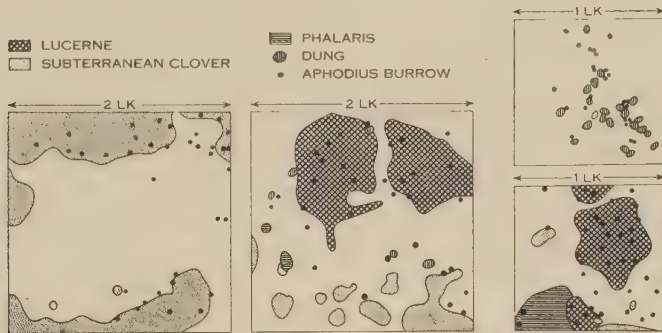

Fig. 11.—Examples of distribution maps of occupied larval burrows in relation to the distribution of vegetation and dung. The burrows were first located by probing with plastic rods; their occupation confirmed by subsequent examination of each burrow.

There is also a conspicuous trend to heavier infestation towards block A. During the work of sampling, it was consistently noted that the soil became moister and slightly deeper, moving from block F towards block A. It may be significant that, although there was no response by the pasture to any of the fertilizer treatments, there was a marked gradient in pasture yield, which increased from F to A. This evidence suggests that either the denser vegetation *per se*, or its causative factors, made the site more favourable for oviposition towards block A.

The two density gradients are so marked that any correlations existing between larval ·density and the various factors measured were probably masked. In a thorough statistical analysis of the data, the only significant result was that the larvae showed a preference for making their burrows in close proximity to plants of lucerne, compared to clovers or grasses (Table 7).

Aggregations of larvae were also demonstrated in other pastures by mapping the distribution of larval burrows in relation to individual plants and pieces of dung. Several typical distribution maps are reproduced in Figure 11.

The preference of the larvae for leguminous as opposed to gramineous material is shown by the fact that the proportion of stored leguminous matter was often much greater than the proportion of that element in the pasture, whether this was calculated on an area or a weight basis.

(iii) *Discussion.*—From the data presented above certain facts concerning the distribution of the species emerge. Firstly, within the climatic area suited to the species, its presence or absence in pastures is largely determined by the botanical and physical nature of the latter, and by the soil types on which they are developed. At the other extreme, the "microdistribution" of larvae can be accounted for in terms of the burrowing habits of the adult females and of the food preferences of the larvae. To some extent, the irregular distribution of patches of high larval numbers can be attributed to the visual attraction of the adult towards objects such as trees or fences. There still remains the problem of accounting for irregular distribution in uniform level pastures. The author developed an hypothesis that this was due to the chance settling of swarms of gravid females, but was forced to abandon this when accumulated data suggested that such females do not fly in swarms but act independently in their search for an oviposition site. The most convincing evidence against this hypothesis was provided by studies on the distribution of developmental stages in samples from patches of high larval numbers. If such patches resulted from oviposition by swarms of females entering the soil simultaneously, one would expect that the larvae in any one patch would be mostly in the same instar; also, that significant differences would be found to occur between the developmental states of larvae in different patches, according to whether the parent swarms had occurred early or late in the flight season.

In all the larval samples taken, the range of developmental states was very considerable, far greater than could be accounted for by chance variation in the rates of development of individual larvae of similar age. The data for several samples are given in Table 8.

It would seem that gravid females fly to particular sites throughout the whole flight season, and that these sites must therefore have some characteristic that permits their recognition by the females. The special properties of these areas may be due to factors not recognized by the author as influencing *Aphodius* adults. The only alternative possibility seems to be that the females possess some highly developed olfactory or auditory mechanism whereby they can detect the presence of other females, or possibly larvae, in the soil. Oviposition in a pasture that is uniform to the human eye might at first be more or less at random but if

by chance, certain areas were selected by relatively greater numbers of females, that area would thereafter be possessed of a bias favouring its selection by later females, the bias increasing very rapidly with time. The problem is extremely difficult to study and remains unsolved.

V. MORTALITY FACTORS

Due to sampling difficulties caused by the rapid disintegration of dead larvae in the soil, and to the slow movement of larval populations during their development, it is not easy to make an accurate assessment of larval mortality in the field. The general trend as revealed by repeated sampling of infested areas is an abrupt decline of numbers with time.

TABLE 8

DIFFERENCES IN THE RATE OF DEVELOPMENT OF APHODIUS LARVAE IN DIFFERENT HABITATS
Percentage of larvae in each stage

Stage of Development	Dickson Experiment Station, A.C.T. 29.iii.49				Golf Links, Canberra, A.C.T. 4.iv.49
	Sample A	Sample B	Sample C	Sample D	
First instar (late)	—	1	—	—	—
Second instar (early)	14	48	45	19	—
Second instar (medium)	22	32	48	53	—
Second instar (late)	53	11	4	20	4
Third instar (early)	6	7	2	6	20
Third instar (medium)	5	1	1	2	53
Third instar (late)	—	—	—	—	23

Dispersal of larvae from patches of high density was observed to be of the order of from 3 to 6 ft over the whole season, irrespective of the size of the patch. Such movement results in a decline of density per unit area within the patch that may introduce an error into estimates of density changes due to mortality. The extent of this error will naturally vary inversely with the initial size of the patch. Study areas were therefore selected in which the infested patches were large, and in which there was a minimum of sparsely occupied, or unoccupied, space. Sampling stations were randomly distributed within these areas.

Initial densities as high as 300-400 larvae per sq. lk were recorded. However, irrespective of the initial density level, that of the adults produced rarely exceeded, and was often less than, 8-10 per sq. lk. Typical examples of population density–time curves are shown in Figure 12. Difficulty was experienced when an attempt was made to obtain large numbers of immature adults from insectary-reared larvae; mortality in crowded cultures was severe and the maximum number of adults produced was of the same order as that found in the field. These observations suggest the existence of mortality factors the operation of which increases

in severity with population density, thus providing a powerful density-stabilizing mechanism.
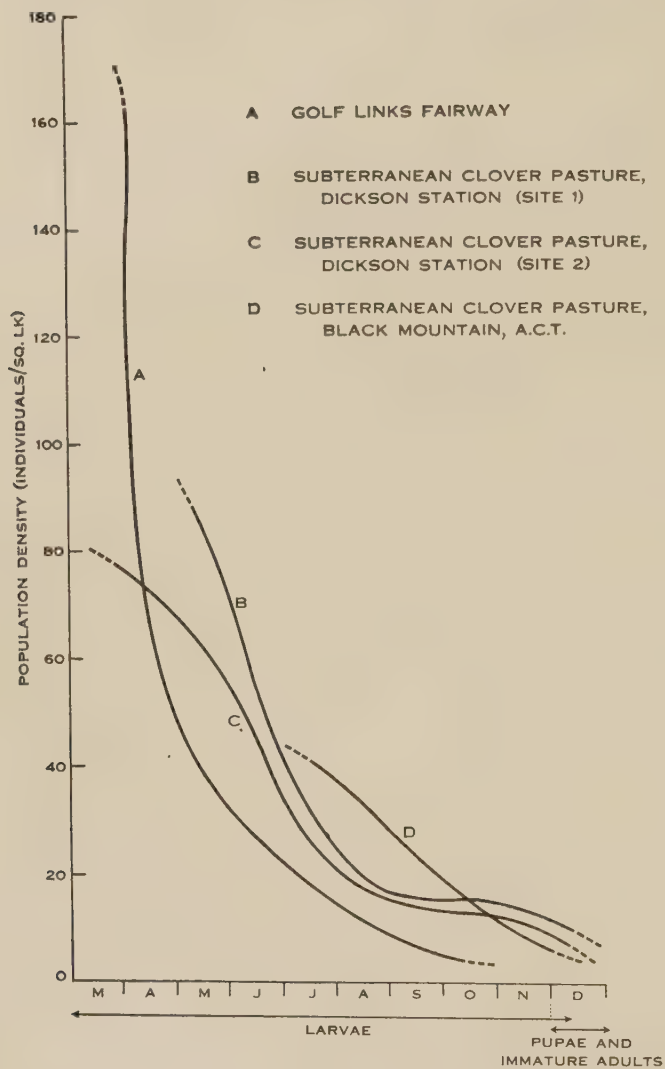

Fig. 12.—Population density curves of *Aphodius* in four situations in Canberra in 1949. The study areas in each site were approximately 1 acre in extent and were selected for their uniformity of infestation. Mean population densities were estimated at fortnightly intervals from a number of samples randomly distributed throughout each pasture.

If a value of 200-250 is taken as a fair estimate of the average initial density in patches of heavy infestation, then the overall mortality of the immature stages is of the order of 95-96 per cent. It is of interest

to note that, having a reproductive capacity of the order of 25 (see Section III(*b*)(v)), a 4 per cent. survival would be required to provide for the maintenance of the species at similar density levels in successive years.

A number of factors was found to cause mortality at different stages in the life-cycle of the insect and these are now discussed.

(a) *Description of the Known Mortality Factors*

(i) *Larval Combat.*—It was found that the most common cause of larval mortality was damage to the epidermis, resulting from physical combat between larvae when they are foraging on the pasture surface. Minor punctures result first in local lesions and then in systemic necroses due to invasion of the tissues by soil-inhabiting bacteria. Major punctures incapacitate the larvae to such an extent that they are unable to burrow into the soil and die as the result of desiccation or predation by birds.

Despite the crowding of larvae in the oviposition cell immediately after hatching, no combat was observed at this stage. However, when larvae have formed individual burrows, they show great irritation at contact with each other and slash aggressively with their mandibles. When first hatched, the mandibles are still rather soft and may be incapable of inflicting damage; dispersal from the oviposition cell may well be stimulated, not only by hunger, but by the onset of combat. Under natural conditions larvae do not come in contact with each other except when foraging. At this time. their density on the pasture surface may be as high as 3-4 individuals per sq. in. Frequency of contact is very high and mortality considerable. After the first few contacts, the larvae snap at others touching them, and engage in remarkably active combat. The damage inflicted is most commonly puncture of the thoracic sternites, or amputation of the legs or antennae.

The importance of combat as a mortality factor may be illustrated by reference to two experimental plots, each 8 × 8 ft, on a subterranean clover pasture at Dickson Station. Plot *A* was entirely surrounded by metal troughs, arranged so as to trap all larvae moving out of the plot and to prevent larvae moving in from outside. Plot *B* was surrounded by vertical metal barricades that prevented movement in either direction. In plot *A*, the mean population density of the larvae decreased from 78 to 14 per sq. lk from April 20 to August 16, 1949, an estimated loss of 9216 larvae. This loss was almost exactly counterbalanced by the total of 9348 larvae trapped in the troughs. The population density was at no time very high, and the regular removal of larvae from the plot by trapping presumably kept the density below that level at which conflict would have become a serious mortality factor. With growth, the threshhold density for conflict becomes lower, so that confining larvae to a fixed area of turf is equivalent to increasing their density over a period of time. This was the situation in plot *B*, where the population decreased

from 90 to 17 larvae per sq. lk over the same experimental period, an estimated loss (in this case, mortality) of 11,600 larvae. Other mortality factors were insignificant in their effects over the period of the experiment and all the larvae trapped from plot *A* were active, healthy specimens. Consequently most, if not all, the mortality in plot *B* is attributed to the effects of crowding and the combat which results from it.

In heavily infested pastures, where initial population densities range from 100 to as many as 400 larvae per sq. lk, severe mortality occurs although there are no physical barriers to prevent dispersal. Observations showed that the rate of dispersal is too slow to prevent combat from occurring.

(ii) *Effects of Weather Factors.*—The species is remarkably resistant to extremes of temperature and to flooding. However, when the larvae are foraging, a sudden heavy shower of rain may pelt them into a muddy surface. If the rain ceases and the mud dries and hardens rapidly, many of the larvae become embedded and are quite unable to extricate themselves. On several occasions, thousands of larvae were seen on the surface the morning after a night when foraging took place; all of these died from exposure or from predation by birds.

(iii) *Bacterial Diseases.*—The incidence of bacterial diseases is associated with larval combat and with high soil moisture. Disease occurs most frequently in dense populations of larvae, the organisms entering the tissues through punctures in the skin suffered in the course of combat. Necroses commonly begin at the stumps of amputated legs, antennae, or in the damaged tissues of the thoracic sternites. Discoloration spreads rapidly over the dorsal portion of the thorax, and along the abdomen. Smears of the larval blood showed that the dominant organism was a spore-forming rod bacillus of the drumstick type. A spore suspension was prepared by triturating diseased larvae and the product clarified by filtration. A dose of 0.1 ml of the suspension was injected below the mesothoracic tergites of a series of healthy larvae. These were incubated at 25°C and all developed typical necroses within 12 hr and died within 2 days. Some soil was then treated with the spore suspension; this was used as a substrate for a further series of cultures. In some, 20 healthy larvae were introduced, in others, individual larvae. Of the former series, all the larvae died within 2 weeks, while the incidence of the disease in the individual cultures was nil.

Irrespective of their population density, a high soil moisture level appears to increase the susceptibility of insects to bacterial diseases (Andrewartha and Birch 1954). Most of the mortality in insectary cultures of miscellaneous scarabaeid larvae maintained by the author was due to diseases of this type; their incidence was very clearly associated with excessive soil moisture. In the course of field surveys on the distribution of *Aphodius*, bacterial diseases were recorded particularly in damp situations, e.g. near the altitude limit of the species in alpine

regions, and in the wetter parts of its range near the New South Wales coast. In comparable situations in Canberra, bacterial diseases were found to be more prevalent in wet than in dry seasons.

(iv) *Fungal Diseases.*—The outstanding characteristic of the fungal diseases recorded was their high incidence in populations occupying sites that had a history of previous high population density. The oviposition behaviour of the adults is such that populations tend to recur in particular patches of pasture in successive years, although new patches are occupied each year in addition. The old patches gradually lose their identity with successive generations and eventually support only a very low population density.

That fungal diseases are not serious mortality factors in newly infested areas* may be due to an insufficient density of spores. Spores of certain pathogenic fungi may, however, remain viable in the soil for some years. This was discovered accidentally when 40-50 per cent. of the larvae in experimental cultures succumbed to the disease. The soil used had not been sterilized and was taken from a site where *Aphodius* had been especially abundant 2 years previously and where *Cordyceps* infection had been common. In cultures of the same soil type taken from an adjacent site where *Aphodius* had not been present the incidence of the disease was negligible.

Three fungal diseases of the immature stages were noted:

(1) *Cordyceps aphodii* Mathieson.—A description of this fungus and an account of its behaviour in the host larva is given by Mathieson (1949). The incidence of the disease in the field is referred to by Twentyman and Pescott (1942). Very little is known of its epidemiology. Macroscopic symptoms are shown only by the third instar larva, which becomes sluggish, dull, and somewhat opaque. The larva dies and its colour changes to a characteristic pink, thence to a dirty yellow. The mummified larva is extremely hard and persists in the soil without disintegration for several years. At the pink stage, fruiting structures of the fungus appear; these are numerous and may protrude from any part of the body but most frequently about the head. The stromata extend until they reach the soil surface, where a clubbed spore-bearing organ is exposed. It is interesting to note that infected larvae die, not at the bottom of their burrows, but within an inch or so of the surface. Stromata were found to range in length from $\frac{1}{4}$ to $1\frac{3}{4}$ in. The mortality of third instar larvae from this disease often exceeded 50 per cent.

(2) A *Metarrhizum*-like fungus that causes severe mortality in the later immature stages, especially the diapausing larva and the pupa. It was observed to be especially common in the lighter soil types inhabited

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* "Newly infested" here refers to pastures developed on areas that were previously unsuited ecologically to *Aphodius*, or areas of permanent pasture in which all signs of previous infestation have been obliterated.

by *Aphodius*. In common with bacterial diseases, both this fungus, and *Cordyceps,* appear to be more common in wet than in dry situations.

(3) A fungus that destroys egg batches in the soil, causing them to become hard and leathery in texture. Unsuccessful attempts were made to isolate the organism responsible from various contaminants. The disease was recorded only on three occasions, but owing to the relatively small number of samples taken of the egg stage, it is not possible to assess its importance as a mortality factor.

A fungus, tentatively identified as an *Empusa,* infects adults when these are feeding in the dung pads. Characteristic of the disease are the dense white fungal structures that penetrate the intersegmental membranes and grow until they almost conceal the host. The proportion of adults infected was found to range between 3 and 5 per cent. of the population in a pad.

The spores of *Cordyceps* or *Empusa* (?) may be dispersed by adhering to the outer surfaces of adult beetles. In burrowing in dung pads and in moving over the surface of the soil, the beetles must frequently come in contact with the spore-bearing structures of these organisms. The spores may also be dispersed by wind, or be washed into the surrounding soil by rain. The spores of the *Metarrhizum*-like fungus are produced below the surface of the soil. They are probably well distributed through the soil by the burrowing of subsequent larval populations and it is possible that they might also be transported by adults, as these have to burrow to the soil surface before taking to flight.

(v) *Nematode Infection.*—Occasional parasites of the larvae are nematodes of the genus *Mermis*. These can be seen through the abdominal cuticle, coiled about the hindgut. The host does not appear to suffer injury from their presence until such time as the parasite penetrates the body wall and leaves the host to encyst in the soil. Secondary bacterial infection then often follows. The nematodes live a free existence in the soil for much of their life-cycle. At times they leave the ground and can be found, in large numbers, festooned on overhanging vegetation. Such activity occurs only .under very wet humid conditions. The nematodes produce eggs which lie free in the soil; it is thought that the hatching of these is stimulated by the gastric fluids of the host larva and that the young nematodes then penetrate the gut wall and lie freely in the haemocoele. A related species of *Mermis* has been recorded as a parasite of earwigs (Crowcroft 1948).

(vi) *Predators.*—(1) Thynnid wasps: Wasps of the subfamily Thynninae attack a wide range of scarabaeid larvae. A species determined by Mr. B. B. Given as *Tachynomyia* sp. appears to be specific to *A. howitti*. Parasitism occurs in the late larval stage, after damage to pastures has ceased. Mortalities as high as 40-50 per cent. have been recorded.

The adult males of *Tachynomyia* feed on eucalypt blossom or on the exudates of scale insects. The females do not travel to the food source but remain in the soil and are fed by the males which carry surplus food to them. The female oviposits on the ventral surface of the host larvae. The parasite larva is a gross feeder and completely destroys the softer structures of the host. The feeding stage is short, the parasite then forming a cocoon about itself in which it subsequently pupates. The remains of the head capsule of the host larva are often found attached to the fibrous outer layers of the cocoon. While the flight range of male *Tachynomyia* is considerable, the incidence of parasitism is naturally related to the proximity of the trees on which they feed. Appreciable parasitism has not been recorded in *Aphodius* populations more than several hundred yards distant from trees.

(2) Miscellaneous predators: *Aphodius* larvae may form part of the diet of such polyphagous predators as the larvae of asilid flies and carabid beetles. The usual method of attack is by puncture of the head capsule. In a few instances, large numbers of asilid larvae were found where *Aphodius* larvae were the only suitable prey available.

Birds, especially magpies (*Gymnorhina* sp.), destroy a large number of larvae particularly in early winter when these are small and near to the soil surface. The birds appear to prefer melolonthine larvae to those of *Aphodius* and severe predation by them has never been observed in pastures where *Aphodius* was the predominant element of the scarabaeid fauna.

Several species of night-flying birds take adults when flights are in progress but the mortality caused is probably negligible.

(vii) *Mortality Due to Unknown Causes.*—Adult females that have completed primary oviposition are often found dead on the pasture surface, or near dung pads, but show no sign of disease or parasitism to account for their deaths. It is suggested that death may be due to physical exhaustion. Beetles at this stage possess very small energy reserves. The fat-body is used up in the development of the first batch of eggs and the gut is empty. Such beetles must depend for survival on finding food without delay. Probably those found dead failed to do so in time, or having arrived in the vicinity of food, were too weak to feed. As females lay most of their eggs before feeding, such mortality can scarcely be of great significance in regulating the numbers of the species.

(b) *Factors Involved in Population Regulation*

In Sections IV and V of this paper, a number of factors affecting the distribution and abundance of the species have been described. It remains now to attempt a synthesis, to build up a broad picture of the regulation of *Aphodius* populations, to classify the various factors, and to make an assessment of their relative importance in the ecology of the insect.

The overall situation may be summarized as follows:

(1) Like most insects, *Aphodius* produces a large surplus of offspring and so tends to multiply.

(2) Mortality is low in uncrowded situations except where these contain an accumulation of fungus spores due to previous heavy infestation.

(3) Mortality is severe in crowded situations, mainly due to larval combat which increases in frequency with crowding; this mortality approximately counterbalances the surplus of offspring produced.

(4) As the mortality in crowded situations varies directly with larval density, the number of adults produced per unit area *of the crowded zones* is approximately constant.

(5) The size, number, and distribution of the crowded zones is determined:

   (a) By the favourability or otherwise of the various situations which form a mosaic within the distribution area.

   (b) By a behavioural characteristic which causes heavy oviposition within certain areas although these do not seem any more favourable than many other areas in the vicinity.

(6) Both in time and in space, climatic, edaphic, and vegetational influences vary the favourability of the environment, and presumably also vary the local factors which influence the selection of particular areas for heavy oviposition. Consequently (from 4), the abundance of the species within its whole area of distribution must be expected to vary in relation to the changes of these factors, as is observed.

(7) These observations demonstrate the existence of density-induced mortality which can regulate populations at densities related to the prevailing conditions.

Thus the behavioural characteristics of *Aphodius* appear to limit its populations far below the intrinsic capacity of the environment. Firstly, there may be little or no oviposition in large parts of the distribution area which appear just as favourable for larval development as are the overcrowded parts. Secondly, even in densely occupied areas in which there is severe mortality due to combat, a proportion of the food may remain uneaten and there is a considerable surplus of space for burrows.

Nicholson (1954) has classified the factors involved in the population regulation of animals. He recognized two kinds of regulating factor: those which are both density governing and density legislative in function and those which are purely density legislative.

Density governing factors, while permitting population growth when numbers are low, sooner or later oppose and prevent further increase.

They increase mortality or decrease natality as the population density rises, so progressively reducing the excess of surviving offspring, as compared with the parent generation, towards zero. In addition, such factors always have a powerful legislative function. For example, if the food supply is doubled, the limiting intensity of competition will be reached only when the population density is also doubled; or if a fall in temperature reduces the number of offspring produced, a lower intensity of competition will destroy this reduced surplus, and so the population density will be automatically adjusted at a lower level.

Some workers have misinterpreted Nicholson's emphasis on density governing factors as implying that factors uninfluenced by population density are of minor significance in population regulation. As Nicholson has pointed out, when the same density governing factors operate throughout the range of an animal, differences in its population density at different places within the total area occupied may be almost entirely due to local differences in the purely legislative factors, e.g. rainfall.

The density distribution of *Aphodius* populations is characterized by comparatively small areas of very high population density irregularly dispersed among more extensive areas of much lower density. This pattern changes slowly with time and areas carrying low densities of the insect in one year may be highly populated in another. While it is possible that as yet unrecognized regulating factors may operate in low density areas, it is believed that a reasonable account of the limitation of numbers of the species can be given in terms of those operating in areas of high population density. These are now discussed in the light of their possible roles as governing or purely legislative factors.

(i) *Density Governing Factors.*—Density-induced combat, a form of competition for free space, is the outstanding density governing factor affecting *Aphodius* populations. Depletion of food within the infested patches appears to be a complementary governing factor in that it lengthens the time that larvae have to spend on the surface searching for food, and so increases the likelihood of combat occurring. Theoretically, competition of this kind could be an efficient density-stabilizing mechanism, i.e. it could result in the number of survivors per unit area being approximately constant, irrespective of the initial population density, so long as this exceeded a certain minimum. Field observations certainly suggest this to be so (Fig. 12).

Fungal diseases (e.g. *Cordyceps aphodii*) may be regarded as complementary governing factors having a tardy type of reaction. The incidence of disease is not associated with prior damage to the host tissues, but with an abundance of spores of the pathogen in the soil (i.e. with high preceding host density). In the absence of combat, fungal diseases could probably govern population density, although the density level at which adjustment occurred would probably be higher.

Depletion by adults of available dung may be regarded as a minor complementary governing factor, for in the absence of a dung feed the beetles die and do not produce a second batch of eggs. Such depletion reduces the total number of eggs laid, i.e. with increasing density natality is reduced, so decreasing the surplus of offspring requiring to be destroyed by competition for population limitation. As females do not feed until after their first batch of eggs is laid, dung depletion could not by itself govern the population; however, it is more than purely legislative in its action.

(ii) *Purely Legislative Factors.*—The behavioural characteristics of the species are obviously of dominant importance in population regulation and are such that the governing factors operate severely on populations when none of their requisites is significantly reduced within the total favourable area. Between patches of high population density there are nearly always areas of favourable environment, but due to the oviposition behaviour of the adults, both free space and food may be reduced to a limiting degree within the patches.

At the time of oviposition site selection, these patches must presumably possess some characteristic, or "guide mark" that permits the beetles to recognize them. The density of such guide marks, and the ability of the beetles to perceive them, are legislative factors of great importance. Theoretically, maximum competition, and therefore minimum density, would result if all the beetles laid their eggs in the same site. The nearest approach to this ideal situation will be when most of the beetles encounter only one guide mark in the area they search during pre-ovipositional flight. If the guide marks are more numerous, oviposition will tend to be correspondingly dispersed, competition reduced, and density increased. In other words, population density might be expected to vary directly with the frequency of guide marks above a certain minimum value. Maximum densities could be expected either when guide marks are very numerous, or when they are so rare that few beetles encounter one of them: under such conditions oviposition would tend to be most nearly at random and competition least.

Another conspicuous legislative factor is the bacterial disease that infects damaged larvae. Except possibly under very wet conditions it has no capacity to govern population densities, for it normally kills only those larvae that have already suffered injury in combat. In the absence of the disease many such larvae would recover and the density level at which combat would bring about adjustment would necessarily be higher.

Apart from such minor purely legislative factors as the drowning or possible desiccation of larvae, weather factors, together with soil and pasture type, play a legislative role through their influence on the amount of suitable vegetation in the whole area, which in turn influences the intensity of combat.

Parasites are only of minor importance, being restricted to areas favourable to their adults. Birds act merely as instruments of destruction, sometimes replacing bacterial disease. No predator appears to be of appreciable significance in density regulation.

VI. Conditions Favouring the Development of High Numbers

It has been pointed out earlier that the frequency of occasions of combat is determined by the distribution of rainfall in time, and that the susceptibility of larvae and pupae to disease is increased by wet conditions. As the density governing factors, combat and fungal disease, are common to *Aphodius* populations throughout the range of the species, it is to be expected that fluctuations of annual abundance will be highly correlated with weather conditions.

Evidence was obtained suggesting that dry conditions are not unfavourable to the species. Drought mortality of eggs, diapausing larvae, and pupae are unlikely to be severe, as these stages are protected by the cells in which they live and can probably adjust their own microclimates to a considerable extent (Fidler 1936). Small larvae, making their first burrows to the surface, might be more susceptible to desiccation, yet marked resistance to drought by this stage was observed in the Western District of Victoria in 1951. Until the second week of April, drought conditions had been experienced in this district for more than 12 months. In average years, *Aphodius* larvae would have been mostly in the second instar at this date, in the third instar in especially favourable seasons. Yet in 1951, only first instar larvae were present, although oviposition and hatching had taken place at the usual time. Following the breaking of the drought in mid April the larvae grew rapidly and entered the third instar by June. As the general level of the population was higher in 1951 than in 1950, it seems unlikely that the larval mortality of the first instar was abnormally great.

Attempts were made to obtain records of years of severe infestation in the past, together with meteorological records for the districts concerned. It proved extremely difficult to get reliable data of this kind and the only really useful set of data obtained was that supplied by Major P. J. B. Osborne of "Currandooley", Bungendore, N.S.W. On this large property (18,000 acres) detailed weather records have been kept since 1925, together with notes on the severity of *Aphodius* damage on various parts of the property. Over the period 1925-48 only 4 years of widespread severe damage were noted. In Figures 13(a) and 13(b) the rainfall data for the periods 1939-48 and 1929-31 are illustrated. The average annual rainfall at "Currandooley" over the whole period was 24.62 in., the extremes being 10.03 in. in 1944 and 48.97 in 1934. The annual rainfall in the years of severe infestation was as follows:

<table>
<tr><td>1930—21.11 in.</td><td>1946—19.62 in.</td></tr>
<tr><td>1945—24.51 in.</td><td>1947—22.73 in.</td></tr>
</table>

These years are characterized, not only by the closeness of their total rainfalls to the mean, but by the absence of very heavy falls in any one month. From Figure 13(a) it can be seen that during the three years 1945-47, the monthly totals were (except for April 1945) appreciably less than 4 in. There were some years, e.g. 1942, when climatic conditions were similar, yet the population level of the species was low. However, with an insect having an annual life-cycle and a comparatively low reproductive capacity, abrupt transitions from very low to very high densities cannot be expected; a series of favourable years will be necessary to allow the increase of the population to very high densities.
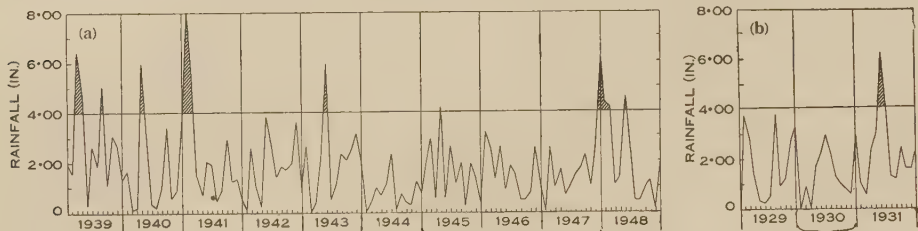

Fig. 13.—Diagrams showing the monthly rainfall totals for "Currandooley", Bungendore, N.S.W. Figure 13(a) covers the period 1939-48; Figure 13(b) covers the period 1929-31. The bracketed years are those in which *Aphodius* was extremely numerous. The hatched portions of the diagram indicate months in which the rainfall exceeded 4 in.

If monthly totals of rainfall of less than 4 in. are used as criteria of "favourableness", it may be presumed that the population density was low in early 1941 and that increase in numbers began then, continuing, with perhaps a temporary check in 1943, until really high numbers were reached in 1945. It would be interesting to know if a decline in density began prior to 1948, but the observations on the degree of infestation were based only on broad visual ratings and no discrimination was made between the levels in 1945-47. Following the very wet summer of 1947-48, the population density dropped to a very low level and larvae were actually difficult to find in the winter of 1948.

Figure 13(b) shows the only other outbreak year (1930) preceded by a "favourable" year and followed by an "unfavourable" one, in which the species was again rare.

Further evidence suggesting that years of low rainfall favour population increase is provided by light-trapping data for *Aphodius* adults at Black Mountain, A.C.T. The deviations from the average annual rainfall and from the average total seasonal catch over the years 1949-54 are shown in Table 9. It will be noted that the total catch of *Aphodius* showed a series of alternate increases and decreases, in the opposite direction to similar fluctuations in annual rainfall. The rainfall deviations were also calculated on a quarterly basis. The rainfall and catch deviations

showed similar negative correlations for all except the July-September quarter.

Canberra and Bungendore are only some 20 miles apart and have very similar climates. The available data, while regrettably meagre, suggest that rainfall data, in conjunction with density estimates of current populations, might provide a means of predicting the probability of severe infestations, in time for preventive action to be taken. However, the species is an economic pest in areas of much higher rainfall, where falls of less than 4 in. in any one month would be exceptional. The correlation

TABLE 9

TOTAL LIGHT-TRAP CATCHES OF APHODIUS AT BLACK MOUNTAIN, A.C.T., IN RELATION TO THE RAINFALL OF THE PRECEDING YEAR, AND THE RELATION OF THESE DATA WHEN EXPRESSED AS DEVIATIONS FROM THEIR RESPECTIVE MEANS

Year	Total Rainfall (in.)	Total *Aphodius* Caught in Subsequent Summer	Rainfall (in.) (deviation from mean)	Trap Catches (deviation from mean)
1949	28.50	5748	—1.07	+918
1950	43.31	2920	+13.74	—1910
1951	23.32	5066	—6.25	+236
1952	40.48	2174	+10.91	—2656
1953	20.69	8245	—8.88	+3415

between dry years and subsequent high densities, suggested by the above data, is probably valid only for a comparatively small district. It is possible that in districts near the low rainfall limit of the species, the correlation might be reversed, exceptionally wet years favouring increase in numbers. Unsuccessful efforts were made to obtain reliable records of past infestations from properties in other parts of the range of *Aphodius* for comparison with the Canberra and Bungendore data.

VII. Conclusions

(a) *Present Economic Status of the Species*

The relationship between pasture yield, species composition, and the animals feeding upon it is extremely complex. The output of the pasture is determined by seasonal weather, soil type, fertilizer treatments, the density of the animals it supports, and their grazing habits, etc. When the demand on the pasture exceeds its powers of regeneration, a marked disequilibrium occurs and the process may become non-reversible. Over-grazing and the partial destruction of pastures leads to changes in species composition and to soil erosion. In any particular instance, the pasture may be able to supply the demands of domestic stock without progressive deterioration, but the infestation of that pasture by *Aphodius*, resulting in a suddenly increased demand when the larvae moult to the third instar, may have quite catastrophic effects. Conversely, a pasture

closed to stock, or lightly grazed, may be able to maintain high *Aphodius* populations without suffering permanent injury. Not only the total demand on the pasture, but the rate of consumption must be taken into account. It is well known that different systems of grazing have distinct effects on the yield and composition of pastures. Intensely heavy demand over a short period may do far more harm than the same total demand spread over a longer period. In Figure 7 are shown the growth rates of two populations of *Aphodius* larvae. The third instar was entered much sooner in one than in the other, the whole feeding stage being much shorter in the former. The destruction of the pasture was almost complete in this instance (Plate 2, Fig. 10), whereas little damage was done in the other pasture (Plate 2, Fig. 11).

Comparable populations may do more damage in the same pasture in one year than in another. This is apparently caused by differences in the patterns of rainfall distribution from year to year. It has been shown that larval foraging activity is controlled by the frequency of falls of rain. In years when falls are frequent and evenly distributed, larval growth is more rapid than when long periods of drought intervene between rainy periods. It is in the former years that damage to pastures is most severe.

The damage done to pastures may be analysed as follows:

(i) Vegetation otherwise available to stock is buried and consumed by the larvae. In years of severe infestation, the average carrying capacity of the pasture is lowered and stock may have to be sent elsewhere on agistment.

(ii) By denuding pastures at a period when growth is slowest, infestations often result in the progressive reduction of their carrying capacity, the original plant species being replaced to some extent by others of less value. The soil excavated by the larvae may completely cover short grass and so reduce its powers of regeneration, particularly as these are slight during the winter months.

(iii) Infestations characteristically occur on rising ground where they favour processes of soil erosion, through the reduction of plant cover and the presence of much loose cast soil that is easily washed or blown away. Extensive sheet erosion is observed on hills that have suffered repeated infestation.

(iv) When stock are forced to graze on infested pastures, they ingest considerable quantities of soil. This is injurious to their health and has been reputed to cause taints in the milk of dairy cattle and excessive culling of young sheep for worn teeth.

It is possible that light infestations have effects that are on the whole favourable. The turning over of the topsoil by the larvae is doubtless beneficial in itself. Occasional instances of previous infestations seeming

to favour the establishment of sown pastures have been noted by Swan (1934) and Evans (1941). The author examined a subterranean clover pasture near Bungendore, N.S.W., which had been re-sown to *Phalaris tuberosa*; due to drought conditions establishment was extremely poor except in those areas where *Aphodius* infestations had been conspicuous in the previous season.

(b) *Probable Economic Status of the Species in the Future*

As the extension of areas of improved pasture seems likely to continue, and the carrying capacity of sown pastures to be increased both by correcting mineral deficiencies in the soil and by the wider use of leguminous pasture species, damage by *Aphodius* can be expected to become severe over an increasingly large area of grazing country.

The availability of insecticides such as lindane and DDT offers a means of economic control of the species at fairly low cost, as these are conveniently applied in admixture with superphosphate when top-dressing is done. The cost of treatment could be reduced by withholding it from those pastures which are unlikely to suffer appreciable damage, either because of inherent ecological unsuitability (e.g. dense pastures of vigorous perennial grasses), or to the vegetation being of a kind that is unaffected by dense populations of *Aphodius* (e.g. lucerne).

(c) *Ecological Control Possibilities*

A number of means of reducing damage to pastures are suggested by a consideration of the ecology of the species:

(i) The use of pastures containing a high proportion of hardy perennial species, either grasses or legumes, which are capable of supporting dense larval populations without suffering appreciable damage.

(ii) The use of the ley system of farming, if clover-dominant pastures are considered essential. As infestations are rarely severe in recently established pastures, a rotation in which clover formed a course of 3 or 4 years' duration should prevent the building up of high population densities.

(iii) The limitation of grazing on susceptible pastures, especially in the summer months. By so doing, the pasture is not brought to a condition approximating to the preferred oviposition site at the time of beetle flights.

(iv) If the essential characteristics of the "guide marks" (see Section V(*b*)(ii)) that determine the pattern of local infestation should prove to be of a kind that can be duplicated artificially, an interesting possibility of ecological control would arise. By distributing such artificial guide marks at an optimum sparseness over areas of susceptible pasture, minimum densities might result from the operation of density governing factors.

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EXPLANATION OF PLATES 1 AND 2

PLATE 1

Fig. 1.—Portion of a severely infested pasture at Black Mountain, A.C.T., in June 1947. The photograph shows the almost complete coverage of the short vegetation by cast soil. The burrow openings are discernible.

Fig. 2.—A heavily infested subterranean clover pasture near Reid's Flat, N.S.W.; the top 2 in. of soil has been removed to expose the larval burrows in cross section. The burrow size may be judged in relation to the leaflets of clover at the top left.

Fig. 3.—Part of an infested patch on a property near Boorowa, N.S.W., showing the great predominance of subterranean clover which results from the infestation of mixed pastures. The photograph was taken in early October 1949, after larval activity had ceased and regrowth was under way.

Fig. 4.—Improved hill pastures near Hill End, N.S.W. The tops of the hills are under clover-predominant pastures and were severely infested. The lower slopes are dominated by native grasses (*Stipa*) which appear white in the figure; they were virtually free from infestation. In the near foreground is part of a sheep camp.

Fig. 5.—A slight depression in a subterranean clover pasture at Dickson Station, A.C.T., in February 1947. It is in such depressions that oviposition occurs very frequently in dry seasons.

Fig. 6.—Another pasture near Hill End, N.S.W. Note the relatively sparse tussocks of natural grass, completely surrounded by a sward of subterranean clover. Oviposition occurred only beneath the clover. Photographed in July 1948.

PLATE 2

Fig. 7.—A panoramic view of the same pasture as that shown in Plate 1, Figure 5, photographed in July 1947. The excavated soil thrown up by the larvae is clearly visible, especially along the edges of advancing fronts.

Fig. 8.—Detail of the pasture shown in Plate 2, Figure 7. Here, two fronts can be seen in the process of coalescence as they move out from a shallow depression on the surrounding level ground.

Fig. 9.—An advancing front, indicated by pegs, which is moving towards the observer; the ground behind the pegs is quite devoid of living vegetation. Black Mountain, A.C.T., June 1947.

Fig. 10.—Detail of a severely infested golf links fairway, Canberra, in April 1947, The destroyed vegetation consisted of annual grasses and several species of clovers and medics.

Fig. 11.—Detail of the *Phalaris tuberosa*–subterranean clover–lucerne pasture at Dickson Station, A.C.T., in which detailed studies of larval distribution were made. The photograph shows part of block *A* (see Fig. 10 and text) where the population density was highest.

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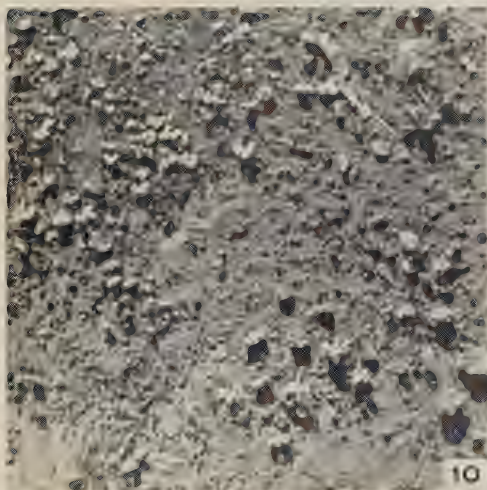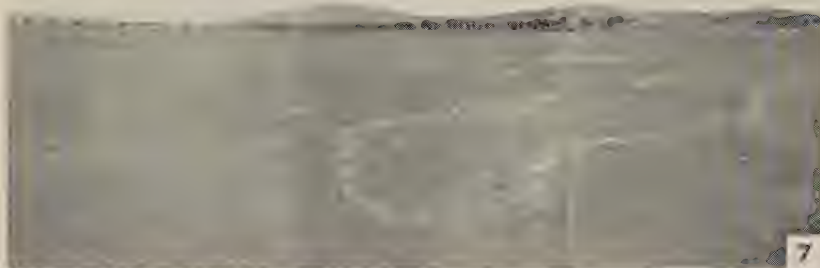
THE ECOLOGY OF *ONCOPERA FASCICULATA* (WALKER) (LEPIDOPTERA: HEPIALIDAE) IN SOUTH AUSTRALIA

I. FIELD OBSERVATIONS ON THE NUMBERS OF O. FASCICULATA AND THE FACTORS INFLUENCING BIRTH RATE AND DEATH RATE

By P. E. MADGE*

Summary

During some years the underground grass caterpillar, *Oncopera fasciculata* (Walker), appears in large numbers and causes severe damage to improved pastures in the lower south-east of South Australia and the Central and Western Districts of Victoria. The present paper, which is the first of several, includes a description of the area of study and an account of field observations on the components of the environment that may influence the survival rate of the species.

I. INTRODUCTION

The underground grass caterpillar, *Oncopera fasciculata* (Walker), is indigenous to southern Australia. In recent years this insect has severely damaged improved pastures in County Grey, in the lower south-east of South Australia, and the Central and Western Districts of Victoria. The species was first recorded in South Australia in 1896 but it was not until 1935 that damage to pastures was reported. Further reports of minor damage in small areas were received in 1937, 1938, and 1940. In 1948, a major outbreak of *O. fasciculata* occurred and large areas of improved pastures were destroyed, with consequent serious economic loss. The outbreak ended in 1950 and damage during 1951-53 was restricted to local situations. However, an increase in the numbers of *O. fasciculata* in 1954 resulted in the insect again becoming of economic importance.

The larvae of *O. fasciculata* feed most actively during autumn and winter. They eat the herbage and straw left from the year before, and thereby reduce the amount of food for the livestock that often have to depend largely on "dry feed" at this time of the year. If the larvae are numerous enough they may consume the young growth as quickly as it appears. In this case the herbage may not make the usual "flush" of growth following the autumn rains, while the soil is still warm.

There is a single generation of *O. fasciculata* each year. Moths fly and mate during the early spring (September-October) and eggs are laid on the ground under pasture plants. Most larvae hatch during late October and early November; they shelter in colonies under silken webbing among surface debris for 2-3 weeks before making individual vertical burrows

* Waite Agricultural Research Institute, University of Adelaide; present address: Department of Zoology, University of Adelaide.

in the soil. When feeding, a larva leaves its burrow and crawls along a silken runway it has spun on the surface of the ground. Although larvae are present from late October until July, evidence of their feeding does not become apparent until April-June. The increased activity of the larvae usually coincides with the germination of annual clovers and grasses following the first substantial autumn rains. Prepupae appear during July-August and pupae during August-September; both stages remain in the burrows.
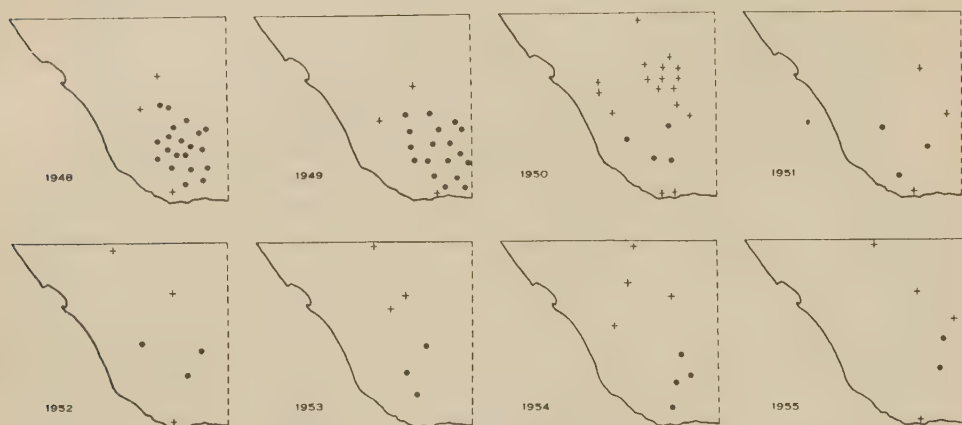

Fig. 1.—Trends in the relative numbers and distribution of *O. fasciculata* in County Grey during 1948-55. Numbers on the well-drained soils are represented by ● and on the poorly drained soils by +. The most important features shown are the changes in distribution from well-drained to poorly drained soils during 1949-50 and the great reduction in numbers in 1951.

So far as may be judged from reports, the outbreak of 1948-50 began quite abruptly in 1948. It seems unlikely that such a large outbreak could result from multiplication during one generation, and it therefore seems likely that the species was in fairly large numbers during 1946-47, even though it was not reported. However, *O. fasciculata* was being studied during the period when the outbreak ended; in 1950 there were large numbers of the species while in 1951 few were found. Field observations during 1950-51 suggested that a marked change in weather, which coincided with the end of the outbreak, might have had some influence on the dramatic reduction in numbers of the species.

Another prominent feature of the 1948-50 outbreak was the pronounced shift in the distribution of the insect from well-drained soils during 1948-49 to low-lying, poorly drained soils during 1949-50. There is evidence that this also might have been caused by the marked change in weather. The relative abundance of *O. fasciculata* in County Grey during 1948-55 and the changes in the distribution of the species are shown diagrammatically in Figure 1. This figure was drawn from data which will be presented in greater detail in a later paper.

Field observations continued from 1950 to 1955 and information obtained was incorporated in field and laboratory experiments done to study the influence of environment on the distribution and abundance of *O. fasciculata* in South Australia. The biology and behaviour of the species also were studied (Madge 1954*a*) and experiments were done on insecticidal control (Madge 1954*b*).

II. General Description of the Area of Study

In South Australia, *O. fasciculata* has been found only in County Grey, the southernmost county of the lower south-east. The south-east is the largest area in the State with an assured rainfall; however, such problems as low soil fertility, seasonal flooding, poor quality native grasses and clovers, and deficiencies in trace elements in many of the soils had to be overcome before large-scale agricultural development could proceed. Projects for the settlement of returned servicemen after World War II have resulted in a rapid development of the district.

(a) Climate

The lower south-east has a Mediterranean type of climate; effective rain falls from autumn to spring or early summer, summers are warm and sometimes humid, and winters are mild. Rainfall is highest (34 in. annual average) in the centre of County Grey and is associated with higher land, but no part of the county receives less than 25 in. Figure 2 shows the distribution of average annual rainfall in County Grey and also will serve as a locality plan for the paper.

The date of the "break" of the season (first substantial autumn rains) varies considerably from year to year and may come as early as March or as late as June. The date of the beginning of autumn rains is important because an early break with good following rains while the soil is still warm causes an early germination of clovers and annual grasses and an increased growth of perennial plants. Winter rains may continue into November or December or the dry period may start in September. The main check to the growth of herbage plants during the summer is lack of moisture.

Mean daily temperatures for July, the coldest month, vary between 9.0°C at Kalangadoo and Penola and 10.5°C at Beachport, situated at the southern end of Lake George; herbage plants continue to grow actively when the mean value for July is above 10°C.

(b) Physiography and Soils ·

The lower south-east is essentially a subcoastal plain (Sprigg 1952). The greater part is less than 300 ft above sea-level and there are no prominent streams. Superimposed upon the plain is a well-developed system of more or less parallel sand-dune ranges which are a series of

beach deposits mainly transverse to prevailing winds. The ranges prevent natural drainage to the sea, and the relatively high winter rainfall, together with surface and underground water moving across from western Victoria, produce extensive seasonal flooding on the low-lying plains. Much of this land was too wet for agriculture until cuttings were made through the ranges.
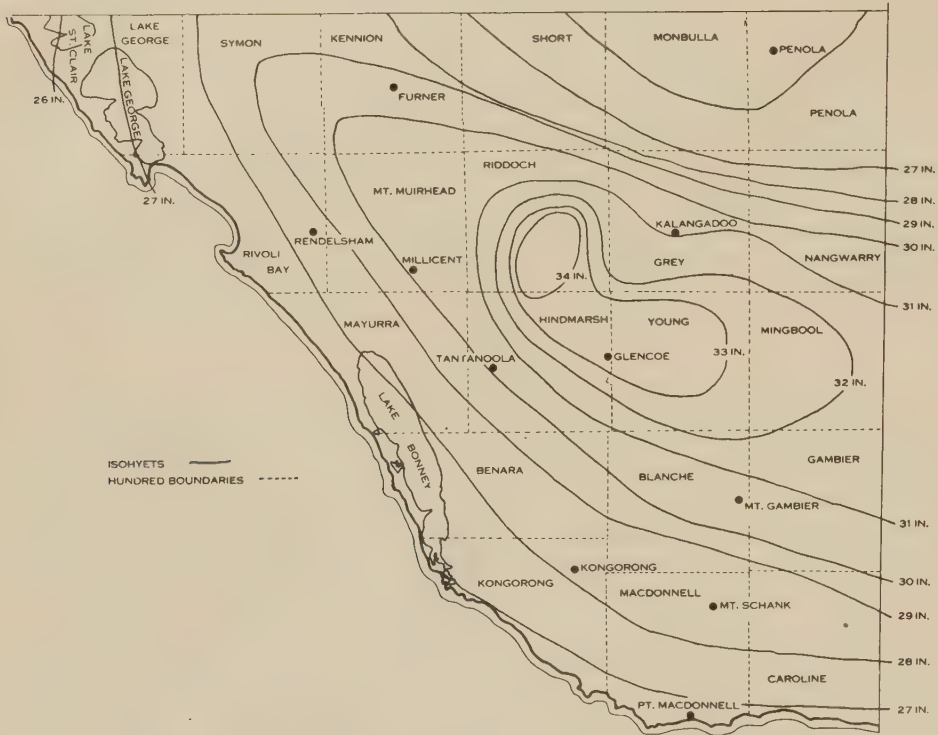

Fig. 2.—Isohyets in County Grey. Also shown are the larger towns and Hundred boundaries (modified after Sprigg 1952).

Plains between the sand-dune ranges are composed mainly of rendzinas—dark grey or black soils, usually found over limestone. (The distribution of soil groups in County Grey is shown in Figure 3.) They were first used for growing cereals (mainly barley) but now support large areas of sown pastures. Meadow podsols are found alongside the rendzina plains and some of the ranges; these soils are sand or sandy loam overlying clay at depths of between 1-3 ft. Terra rossa and volcanic soils occur as well-drained sandy loams, loams, and clay loams, and are highly fertile. The volcanic soils are found to a limited extent around Mt. Gambier, Mt. Schank, and the Mt. Burr range. Large areas of podsolized sands are found in the lower south-east; these are aeolian and low in fertility. The rendzinas, meadow podsols, and podsolized sands (where they occur on the plains) may be classed as low-lying, poorly

drained soils. Pastures growing on them have been severely damaged by
O. fasciculata, especially during years with low winter rainfall. During
wet winters, larvae, prepupae, and pupae on these soils are likely to be
drowned. The terra rossas, volcanics, and podsolized sands (where they
occur on the ranges) may be classed as well-drained soils. These soils
also may support a large population of *O. fasciculata,* especially during
years with a high spring rainfall.

Fig. 3.—Distribution of soil groups in County Grey. See text for description of the
soils (modified after Tiver and Crocker 1951).

(c) Vegetation

There are few trees on the rendzina flats, and natural vegetation
consists mainly of tussocky grasses, such as white tussock (*Poa australis*
R. Br.). On the more fertile sandy plains the natural vegetation is a
sclerophyll woodland. The dominant tree is the red gum (*Eucalyptus
camaldulensis* Dehn.), and undergrowth consists of small trees, shrubs,
and bracken fern (*Pteridium aquilinum* (L.) Kuhn). Tussocky grasses,
which are mainly species of wallaby grass (*Danthonia* spp.), are found
on the higher land and there are rushes and sedges on the wetter land.

Sclerophyll heath grows on the less fertile, low-lying sand and is made up mainly of honeysuckle (*Banksia* spp.), yacca (*Xanthorrhoea* spp.), and other low vegetation.

Most of the more fertile, well-drained land has been cleared but the original vegetation probably was characterized by an association dominated by stringybark (*Eucalyptus baxteri* (Benth.) or *E. obliqua* L'Hérit. or both), with honeysuckle, *Acacia* spp., and bracken fern also prominent (Tiver and Crocker 1951). There would have been a ground cover of tussocky grasses. Natural vegetation on the stranded dunes is composed of a dry sclerophyll forest with stringybark the dominant tree. Undergrowth consists of shrubs and small trees, and bracken fern is abundant.

The earliest settlement of County Grey by Europeans was made by graziers who acquired tracts of land for grazing sheep and cattle. As settlement continued, the area of grazing land was increased by the clearing of timber and scrub. Legumes and grasses were introduced into County Grey soon after settlement began but these did not grow well except on the more fertile soils. The practice of sowing improved pastures did not become widespread until the 1920's, following the discovery that superphosphate had to be applied to the poorer soils before introduced clovers and grasses would grow well. Soon afterwards it was found that subterranean clover (*Trifolium subterraneum* L.) was a very valuable plant on some of the poorer soils.

Briefly, stages in the development of improved pastures in County Grey are: artificial drainage where necessary; natural woodland cleared; land ploughed and top-dressed with superphosphate and trace elements (if needed) ; subterranean clover and perennial grasses sown. The grasses usually are Wimmera ryegrass (*Lolium rigidum* Gaud.), perennial ryegrass (*L. perenne* L.), Yorkshire fog (*Holcus lanatus* L.), phalaris (*Phalaris tuberosa* L.), or cocksfoot (*Dactylis glomerata* L.). Sub-terranean clover is replaced by strawberry clover (*T. fragiferum* L.) in the wetter situations.

III. COMPONENTS OF THE ENVIRONMENT THAT MAY INFLUENCE THE SURVIVAL RATE OF O. FASCICULATA

(a) *Weather*

Studies on the biology of *O. fasciculata* revealed what appeared to be two critical periods during the life-cycle of the insect. In one case the egg and young larva, being on the surface of the ground, might be exposed to evaporation; this is more likely to happen on the well-drained soils. Results of experiments on the influence of dryness on the survival rate of the eggs and larvae will be discussed in later papers.

(i) *Excessive Wetness.*—The other critical period during the life-cycle of *O. fasciculata* appeared to be during the mature larval, prepupal,

and pupal stages when individuals might be exposed to excessive wetness during the winter if situated on the low-lying soils subject to flooding. As the soil becomes soaked following rain, a larva of *O. fasciculata* at first remains in its burrow, even when the burrow becomes filled with water. After about 24 hr the larva usually comes out. If the surface of the ground is not covered with water the larva shelters in its covered runways and returns to its burrow when the water has drained away. When the ground surface is covered with water, the larva is able to escape drowning by crawling upwards into vegetation extending above the water; if this sort of vegetation is not available the larva remains on the surface under the water and is drowned. A larva will not recover if it has been under water for 48 hr or longer. After the larva has been forced from its burrow and covered runways, the surface water might drain away before the insect has drowned; however, it then has to construct a new burrow and, until it is underground once again, the larva is exposed to predators, of which birds are most important. Also, the larva is weakened by the extreme wetness and may die from this exposure or it may be infected by pathogenic organisms. Although no epizootics were seen, Martyn (unpublished data) found an outbreak of a fungal disease of *O. intricata* Walker in Tasmania and thought it was caused by the unusually wet season.

Many larvae were found drowned in late August 1950, on a property near Kalangadoo. The autumn rains were late that year and rainfall during June and July was below average. However, rain during August was slightly above average and 1.09 in. fell on the 29th and 30th. By the following day it was evident that a large proportion of the larvae living in the lower areas had been drowned. Dead larvae, prepupae, and pupae were found in pools of water on the surface of the ground as well as in areas where the water had drained away. Sampling of the area that had been flooded showed that there were no larvae still in burrows—all had been forced to the surface by the water. Larvae on some of the higher land nearby were still established in their burrows and had not been disturbed by the rain.

Two days later, following further rain (0.85 in.), similar conditions were seen. Land that had not been flooded on the 31st was very wet or under water and there were large numbers of larvae, prepupae, and pupae on the surface of the ground. Magpies (*Gymnorhina tibicen leuconota* Gould) and crows (*Corvus* spp.) were seen feeding in the flooded area and an examination of faeces showed large numbers of head capsules of *O. fasciculata*.

In this particular situation there was no vegetation extending above the water and larvae had no chance to escape the extreme wetness. After leaving their burrows, larvae that survived drowning sheltered under whatever cover was available but were unable to build new burrows because the soil was too wet. From the numbers of birds seen, and the

amount of their faeces on the ground, it appeared that a large proportion of these larvae was eaten. By September-October no larvae, prepupae, or pupae were to be found, and apparently no moths emerged from the flooded situations, for no empty pupal cases or moths were found.

Another example of excessive wetness causing a high death rate among larvae was seen at Eight Mile Creek the same year. This district runs parallel to the coast east of Port MacDonnell and formerly was swamp land, but by 1950 was drained sufficiently for soldier settlement. Before the land was settled it was cleared and cocksfoot and strawberry clover were sown. In 1950 there were large numbers of *O. fasciculata* in this area. Rain during August caused considerable flooding in the district, forcing larvae, prepupae, and pupae from their burrows, and many were drowned or eaten by sea-gulls (*Larus* spp.).

This situation differed from the one at Kalangadoo in that there was vegetation extending above the water, enabling some larvae to crawl upwards away from the water. The paddock in which the observation was made had not been grazed for some time after the pasture was sown and the cocksfoot had developed a large tussocky growth (Plate 1, Fig. 1). Some larvae were living in these tussocks and their runways extended upwards into the growth instead of horizontally along the surface of the ground. As the soil became waterlogged, the larvae were able to crawl up into the cocksfoot tussocks, while most of the larvae living away from the tussocks were drowned or eaten by sea-gulls. The paddock was gently undulating and in some cases larvae that were not living in the tussocks were not disturbed by the wetness because the water did not reach them.

Other examples of excessive wetness reducing the numbers of *O. fasciculata* were seen during this study. The heavy black soils around Millicent are very wet during most winters; *O. fasciculata* has not been found here in large numbers, probably because of the extreme waterlogging. Moderate numbers of the insect were found on this sort of soil in 1951 and the area was examined in July, following a heavy fall of rain. Most of the area where the larvae were living was under water (Plate 1, Fig. 2) and most of the larvae had drowned. The photograph was taken when the weather became clear enough; the flooding had been much more extensive the previous 2 days. The absence of tussocky herbage, together with the flatness of the land, resulted in a very unfavourable situation for *O. fasciculata*.

Excessive wetness also limited the distribution and numbers of *O. fasciculata* at Eight Mile Creek in 1951. In July, larvae were restricted mainly to the lower portions of the paddocks (dry conditions earlier in the year had apparently reduced the numbers on the higher land) and heavy rains that month resulted in a high death rate among larvae. The management of some of the paddocks had improved since the previous year and there were very few cocksfoot plants with a tussocky growth.

Larvae in the lower areas of these paddocks had a smaller chance of escaping drowning than did larvae in the same situations during the previous winter.

(ii) *Low Temperature.*—Temperature does not have an unfavourable influence on the numbers of prepupae and pupae. These stages are found in the field during the winter and early spring and so are not exposed to high temperatures; they remain in burrows about 5-6 in. below the surface of the ground and so are not exposed to low temperatures which may occur at the surface. Unfavourable weather (heavy rain or strong wind) restricts flights of moths but has little direct influence on their numbers. Temperatures are mild during the afternoons but may fall to freezing point at night. There was no evidence from field observations that the temperature was ever low enough to kill many adults.

(b) *Observations on Food and on the Kinds of Places in which* O. fasciculata *Lives*

(i) *Type of Pasture.*—Nearly all the pastures in County Grey have been artificially "improved" by the sowing of exotic clovers and grasses and the distribution of substantial quantities of superphosphate. But small areas of "unimproved" pastures may still be found on some farms, along roadsides, and on stock routes. This vegetation consists mainly of wallaby grass (*Danthonia* spp.) and other perennial and annual grasses; there are few or no clovers. It is probable that this sort of pasture was characteristic of most of the county 40 years ago.

A striking feature of the 1948-50 outbreak was that larvae of *O. fasciculata* rarely occurred in large numbers in places where this sort of vegetation was growing. A typical example of this was seen in the district north-west of Kongorong. A small portion of a large property was bought by the State Government after World War II to be subdivided into blocks for returned servicemen. The blocks were fenced and given liberal dressings of superphosphate and sown with subterranean clover and grasses. During the outbreak large numbers of *O. fasciculata* were found on the improved pastures on the blocks while the adjoining, undeveloped land was lightly infested.

In 1950 many cases were seen where there were large numbers of larvae in a paddock carrying an improved pasture while there were few or no larvae in the area between the boundary fence and the road. Some properties that were heavily infested in 1950 had stock routes running through them and almost invariably *O. fasciculata* was scarce on the stock routes. What appeared to be exceptions were seen but in each case an examination revealed that native growth had been replaced by introduced clovers and grasses.

Vegetation in the unimproved areas usually is upright and sparse and there is a large proportion of bare ground. In this sort of place

it would be expected that eggs and young larvae of *O. fasciculata* would be exposed to an unfavourable environment and the death rate might be much higher than in an area of improved pasture, where the soil is covered by a dense mat of herbage. Also, the food supply would be inadequate because there would be little or no clover and only poor quality grasses.

The sort of place in which moths shelter between flights does not have much influence on their own survival rate but is of great importance in determining how many moths will emerge from these situations in the next generation. If the gravid female shelters (and lays her eggs) under dense herbage, the eggs and larvae have a good chance of surviving an unfavourable environment, but if only sparse herbage is available there may be a high death rate among the immature stages. Also, if the female shelters under herbage in the lower areas of poorly drained soils, the larvae, prepupae, and pupae may subsequently be drowned.

It would appear that most adults that emerge survive to take part in the mating flight and most gravid females survive to lay their eggs. The important contribution the female makes is in the choice of a place in which to shelter after mating, for it is here that she lays her eggs. This behaviour has a direct bearing on the survival rate of her progeny.

(ii) *Interaction of Type of Pasture with Weather*.—Although larvae were numerous in 1950, only a few places were found in which most of the herbage had been eaten and where it appeared that the amount of food available depended on the numbers of larvae. One example was on a property ("Kaladbro") north-east of Mt. Gambier, in Victoria. The manager estimated that about 3000 acres were severely damaged by *O. fasciculata*, and when the property was visited in July this large area carried very little herbage. A few larvae, prepupae, and pupae were found but there were not many, considering the bareness of the ground. It seems that many eggs were laid here during the previous spring and that many larvae had survived long enough to eat practically all the food, and then had died from starvation.

The shortage of food at "Kaladbro" may be explained in terms of an interaction between weather and type of pasture. "Kaladbro" is in typical red gum country, with a low-lying meadow podsol soil subject to extensive flooding during the winter and spring. The winter of 1950 was very dry (as was 1949) and parts of the property which would normally be under water were passable by car. Even in situations where there were not many larvae of *O. fasciculata* the growth of herbage was poor because the autumn rains came very late and were followed by much less rain than usual. Also, these pastures were composed mainly of annual grasses and clovers, with only a few perennial grasses. The combination of a dry autumn and winter and herbage composed mainly of annuals resulted in a shortage of food and as this food was eaten there was very little regrowth. If there had been more rain (enough to promote pasture growth

but not enough to expose larvae to drowning) there probably would not have been a problem of starvation, for there would have been enough food for the larvae to complete their development, as there was at Kalangadoo.

Kalangadoo is in country similar to that at "Kaladbro" and *O. fasciculata* was abundant here in 1950. The larvae at Kalangadoo, however, were not exposed to the same degree of starvation because there was a better quality herbage (more perennial grasses) and there had been more rain than at "Kaladbro".

Another way of explaining the high death rate at "Kaladbro" would be to say that it was caused by the large numbers of larvae which ate all of the food, and only those which emerged earlier or developed faster survived. It is true that the shortage of food can only be expressed relative to the numbers of· larvae. However, the author believes that there would have been enough food for the larvae at "Kaladbro" if the weather had been favourable. In comparing the numbers which survived at "Kaladbro" with those at Kalangadoo it would seem to be more realistic to place the emphasis on the amount of food rather than the numbers of larvae originally in the area.

(c) Parasites and Predators

This study of *O. fasciculata* lasted for 5 years. During this period the author was constantly watching for parasites and predators. No specific parasite or predator of any stage in the life-cycle was found.

The eggs and very young larvae live on the surface of the ground. The young larvae live under a dense mat of silken webbing which may offer some protection from casual predators. Despite the exposed position of the eggs and young larvae the author did not find any predators eating them. The older larvae, prepupae, and pupae live in burrows and it is not surprising that they are usually safe from casual predators. If they are forced to leave their burrows during the day-time large numbers may be eaten by birds. The only circumstances in which this was observed was when heavy rain flooded burrows that happened to have been made in low-lying or poorly drained soil. Many hundreds of soil samples were taken during experiments with insecticides, during yearly surveys, and during field observations, and in only a very few of these were other animals found attacking the insect. An adult carabid (*Scaraphites crenaticollis* Macl.) and an unidentified carabid larva were found feeding on larvae of *O. fasciculata*.

Adults of *O. fasciculata* do not feed and probably have a maximum life of 2 or 3 days. Most moths emerge during the afternoon in early spring and shelter under surface cover until dusk, when they take part in brief flights. The flight behaviour was described by Madge (1954a). Magpies were occasionally seen searching for moths under surface growth. Also, during a flight of moths, magpies were seen making short flights

to catch "dispersing" moths but did not attempt to catch those flying just above the herbage. Very few moths in flight were captured by the magpies because most of the birds had stopped searching for food when the moths appeared. Although magpies eat more adults of *O. fasciculata* than any other predator, the numbers that they eat are negligible. In one paddock domestic ducks were seen searching for moths, and these and other domestic fowl may reduce the numbers of moths in paddocks around farm buildings.

IV. ACKNOWLEDGMENTS

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ECOLOGY OF ONCOPERA FASCICULATA. I

Fig. 1.—Tussocky growth of cocksfoot, *Dactylis glomerata*, in a paddock at Eight Mile Creek. Larvae of *O. fasciculata* living in the tussocks have a better chance to escape drowning than those between the tussocks.

Fig. 2.—Flooding of a heavy, black soil which carries a well-developed pasture. *O. fasciculata* has little chance to escape drowning in this sort of place.

THE ECOLOGY OF *ONCOPERA FASCICULATA* (WALKER) (LEPIDOPTERA: HEPIALIDAE) IN SOUTH AUSTRALIA

II. THE INFLUENCE OF TEMPERATURE AND MOISTURE ON SPEED OF DEVELOPMENT AND SURVIVAL RATE OF THE EGGS

By P. E. Madge*

Summary

Eggs of the underground grass caterpillar, *Oncopera fasciculata* (Walker), are laid on the surface of the ground during the spring and may be exposed to desiccation.

A field experiment showed that there was a higher survival rate among the eggs and early-stage larvae when eggs were placed under tall, dense herbage. The most likely explanation for this result is that the dense cover protected these stages from dryness and heat. Tall, dense cover is found where improved pastures (herbage consisting of clovers and introduced grasses) have not been heavily grazed or cut for hay.

Laboratory experiments showed that the eggs are easily killed by dryness because they lose water rapidly when exposed to evaporation. The median lethal dose for eggs that had completed 15 per cent. of their development was a 43 per cent. loss of water. As the embryo develops, the eggs become more susceptible to loss of water, and water that is lost cannot be regained when free water becomes available.

I. INTRODUCTION

It was mentioned in an earlier paper (Madge 1956) that pronounced changes in the numbers and distribution of *Oncopera fasciculata* in South Australia during 1948-51 seemed to be associated with the weather. The years 1947-49 were characterized by an unusually wide spread of rain during October-December. Since the eggs and young larvae are to be found on or near the surface of the ground during September-December, this suggests that the rapid multiplication of *O. fasciculata* on the well-drained soils during the initial stages of the outbreak of 1948-50 might have been due to an unusually high survival rate among the eggs and young larvae. Conversely, the scarcity of the species between outbreaks may be due, in part at least, to a high death rate among these stages.

Field observations indicated that the survival rate of the eggs might also be influenced by the sort of place where they were situated; high, dense cover appeared to be commonly associated with later damage to herbage by the larvae.

This paper describes a number of experiments on the moisture and temperature requirements of the eggs of *O. fasciculata*.

* Waite Agricultural Research Institute, University of Adelaide; present address: Department of Zoology, University of Adelaide.

II. Fertility of the Eggs

The egg is creamy white when laid but usually turns a dull black within a few hours. Occasionally eggs were found that remained creamy white or did not change colour for many hours. To see whether these eggs differed from the others, 84 such creamy white eggs were placed on a moist surface at a favourable temperature. Of these, 32 became black, 6 grey, 7 speckled grey, and 39 remained creamy white. There was no embryonic development in any of these eggs. It seems that eggs that do not turn black within a few hours of being laid are infertile. Only black eggs were used in the experiments to be discussed, but, as they were collected at intervals of 12 hr, some could have been infertile.

III. Favourable Temperature Range

The survival rate was measured for eggs which were incubated on moist filter paper at 24 constant temperatures within the range 6.3-31.6°C. The criterion for "deaths" was failure to hatch but it is likely that in at least some cases the eggs failed to hatch because they were infertile. There was a small amount of embryonic development at 6.3°C but no larvae hatched, and at 8°C 92 per cent. died. The favourable temperature range was between about 10°C and 22°C; the mortality ranged from 0-25 per cent., with a mean of 8 per cent. (18 observations).

At 26.7°C embryos had developed in most of the eggs and in some cases the larvae were fully formed. Some had tried to rupture their egg-shells but only 39.5 per cent. of the larvae emerged. No larvae emerged at 31.6°C. The high death rate at the higher temperatures might have been caused by injury to the developing embryo and possibly a change in the texture of the egg-shell.

In the field, eggs are exposed to unfavourably low temperatures (mean daily temperature at Mt. Gambier for September is 11.7°C) but these temperatures do not last long enough to injure the developing embryos. They are not likely to be exposed to harmful high temperatures.

IV. Speed of Development at Constant Temperatures within the Favourable Range

Experiments on the duration of the incubation period of the eggs at constant temperatures were done in 1950, 1951, and 1952. In 1952, eggs from Mil Lel, on a well-drained, terra rossa soil, and Kalangadoo, 19 miles away on a low-lying, meadow podsol, were compared. Eggs were of a uniform age (0-12 hr) and were distributed at random among the temperatures used. Eggs were grouped in batches, usually of 100 eggs, and each batch was placed on moist filter paper in a Petri dish, as previous work had shown that few larvae emerged when the eggs were not kept moist. The Petri dishes were placed in air-tight glass jars containing distilled water and the jars were placed in incubators maintained at the

required temperatures. Temperature readings (to 0.1°C) were taken at 9 a.m. each day and the temperature of each incubator was calculated as the arithmetic mean of a number of these readings. Temperatures inside the Petri dishes would not have fluctuated as much as the air inside the incubators; fluctuations in temperatures of the incubators are shown in parenthesis after the temperature readings in Table 1.

TABLE 1

DURATION OF INCUBATION PERIOD OF EGGS AT CONSTANT TEMPERATURES*: COMPARISON OF YEARS AND LOCALITIES

1950 (Mil Lel)		1952 (Kalangadoo)		1952 (Mil Lel)		1953 (Mil Lel)	
Temp. (°C)	Duration (hr) $\log(\bar{y}_t - 10)$	Temp. (°C)	Duration (hr) $\log(\bar{y}_t - 10)$	Temp. (°C)	Duration (hr) $\log(\bar{y}_t - 10)$	Temp. (°C)	Duration (hr) $\log(\bar{y}_t - 10)$
9.8(±0.3)	1.67	8.0(±0.1)	1.86	8.0(±0.1)	1.86	10.0(±0.2)	1.64
12.8(±0.1)	1.39	9.7(±0.2)	1.64	9.7(±0.2)	1.65	13.4(±0.6)	1.23
16.9(±0.3)	0.98	13.0(±0.2)	1.36	13.0(±0.2)	1.36	16.9(±0.3)	0.93
20.8(±0.2)	0.52	14.7(±0.3)	1.18	14.7(±0.3)	1.17	21.2(±0.2)	0.52
25.2(±0.2)	0.00	16.8(±0.4)	0.99	16.8(±0.4)	0.98	26.7(±0.3)	−0.10
		20.1(±0.4)	0.60	20.1(±0.4)	0.58		
		24.5(±0.2)	−0.22	24.5(±0.2)	−0.22		

Regression Equation and Regression Coefficient for Each Set of Data

1950 (Mil Lel)	1952 (Kalangadoo)	1952 (Mil Lel)	1953 (Mil Lel)
$y = 2.77 - 0.1088x$	$y = 2.89 - 0.1196x$	$y = 2.89 - 0.1204x$	$y = 2.63 - 0.1019x$
$b = -0.1088 \pm 0.0032$	$b = -0.1196 \pm 0.0086$	$b = -0.1204 \pm 0.0080$	$b = -0.1019 \pm 0.0029$

* Fluctuations in temperature of the incubators shown in parenthesis.

In the analysis of duration of incubation period for different years and localities, a log transformation (mean duration in hours minus 10) was used and the four regressions on temperature calculated. An analysis of variance showed that the regressions were highly significant ($P < 0.001$) but not the differences between them. That is, eggs from different generations and localities did not differ significantly in their response to the temperatures used. The data are summarized in Table 1.

The combined regression coefficient was -0.1133 ± 0.0036 and was highly significant ($P < 0.001$); the duration decreased by 2.7 hr for each degree Centigrade increase in temperature. The 24 observations (untransformed data) plotted against temperature are shown in Figure 1 and a free-hand curve has been drawn through the points.

V. FIELD EXPERIMENT ON THE INFLUENCE OF "COVER" ON THE SURVIVAL RATE OF EGGS AND YOUNG LARVAE

Eggs of *O. fasciculata* are laid on the surface of the ground, which, in improved pastures, is usually covered with both a layer of surface litter

and a mat of herbage. Unimproved pastures contain much less clover, grasses are more spindly, and there is a large proportion of bare ground; eggs and early-stage larvae living here are more susceptible to desiccation during dry weather.
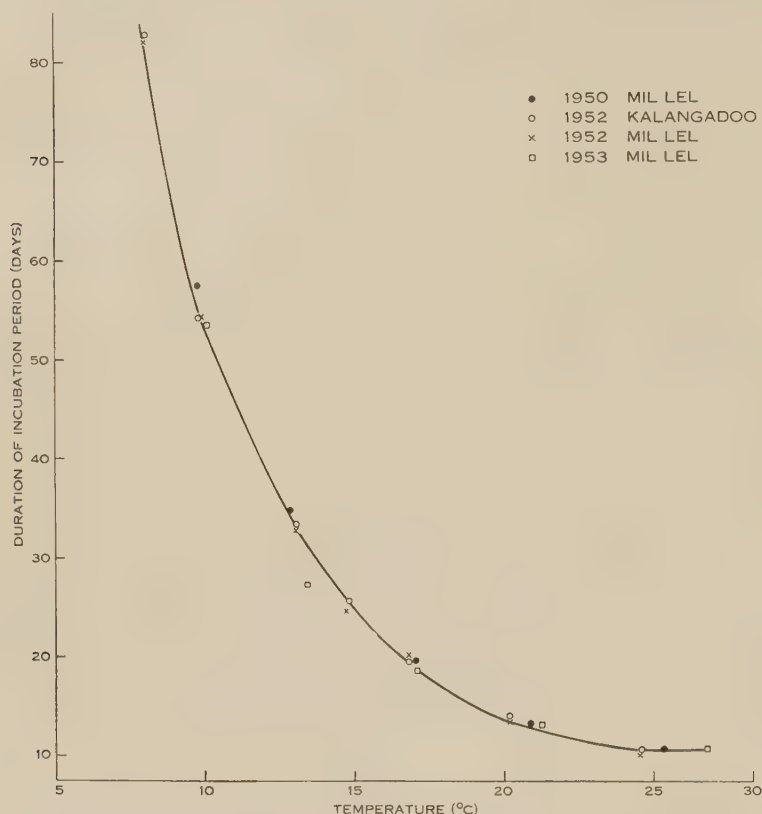

Fig. 1.—Duration of incubation period of eggs of *O. fasciculata* at constant temperatures and on moist filter paper.

In 1951 a field experiment was done to study the influence of cover on the survival rate of eggs and young larvae of *O. fasciculata*. At the same time the experiment was designed to show the influence of both the number of eggs per unit area and the way the eggs were distributed on the chance of survival of individuals under different sorts of cover. A split-plot factorial design was used because there were not enough eggs to try the treatments in all combinations. There were three replicates and each was divided into two main blocks for density (50 and 1000 eggs per sq. yd), each block was divided into two plots for method of distribution (spread evenly over the plot or placed in evenly spaced clumps) and each plot was divided into four subplots for type of cover.

The four types of cover were made by modifying the herbage on the experimental area. Type 1 was untouched herbage and provided a

high, dense cover. In type 2 the herbage was "thinned" by eliminating the dicotyledons with a hormone-type weed killer; this provided a high, sparse cover. Herbage in type 3 was "mown" by clipping it closely with hedge clippers, providing a low, dense cover, and herbage in type 4 was thinned and mown, providing a low, sparse cover.

This experiment was set out in an area where soil was well-drained and the herbage was mainly subterranean clover (*Trifolium subterraneum* L.) and Wimmera ryegrass (*Lolium rigidum* Gaud.). Subplots were 1 sq. yd in size and were separated by metal strips that were pressed into the ground and extended 3 in. above the surface. Both sides of the strips were painted with creosote; these served as barriers to prevent the movement of larvae between subplots.

The eggs were distributed on September 20, when the barrier strips were already in place and the four types of cover had been prepared. Eggs were spread evenly over the subplot or were distributed in groups of 50 eggs; in each case the eggs were placed on the surface of the ground under herbage. The experimental area (48 sq. yd) was covered with hessian during the flight period (September 4-October 8) to prevent the entry of gravid females; this cover retarded the growth of the pasture plants, and probably was favourable for the eggs because it reduced the rate of evaporation from the area.

Under field conditions it was impossible to determine the death rate among eggs separately, so it was decided to determine the death rate among eggs and young larvae together. Accordingly, the numbers of survivors in each subplot were counted in January 1952, when larvae were established in individual vertical burrows in the soil. The method used was developed during studies on the insecticidal control of *O. fasciculata* (Madge 1954).

For analysis of the data, counts of larvae in each treatment were expressed as a proportion surviving from the eggs put on each subplot (zero counts were replaced by 0.25) and the proportions were transformed to degrees in order to equalize the variance (Mather 1951). The analysis of variance showed that there was no significant difference between survival rates of the two levels of density, while both method of application ($P < 0.05$) and type of cover ($P < 0.001$) were significant. The data are summarized in Table 2.

There was a high death rate on all subplots of this experiment; the largest proportion surviving was 22 per cent. on one of the untouched subplots where eggs were scattered. No larvae were found on eight of the subplots that received 50 eggs each, nor on two of the subplots receiving 1000 eggs each. In seven of these 10 subplots the herbage had been mown and thinned.

The most important information obtained from this experiment was that there were more larvae on the untouched subplots (high, dense cover)

than on any of the other types of cover ($P < 0.01$). Also, there were more larvae on unmown and thinned subplots than on mown and thinned subplots ($P < 0.01$). These results show that the survival rate of the young stages of *O. fasciculata* depends on the sort of cover provided by the vegetation in the places where the eggs are laid.

TABLE 2

MEAN SURVIVAL RATE OF EGGS AND YOUNG LARVAE UNDER VARIOUS TYPES OF COVER, DENSITY, AND DISPERSION

Data in degrees

Type of Cover	50 Eggs per Subplot			1000 Eggs per Subplot			Grand Mean Cover
	Grouped	Scattered	Mean Cover	Grouped	Scattered	Mean Cover	
Unchanged	13.84	19.53	16.69	11.52	12.25	11.89	14.28
Thinned	9.92	13.84	11.88	5.49	7.75	6.62	9.25
Mown	5.41	12.03	8.72	3.30	8.19	5.75	7.24
Mown and thinned	4.05	8.18	6.12	3.09	4.33	3.71	4.91
Mean method	8.31	13.40	10.85	5.85	8.13	6.99	
Grand mean	7.08	10.77					

Analysis of Variance between	Minimum Differences for Significance at $P <$		
	0.05	0.01	0.001
Two grand means of cover over all levels of egg density and method	2.87	3.89	5.21
Two means of method for one level of egg density	3.41	5.66	10.59
Two means of cover for one level of egg density	4.07	5.51	7.38

VI. SURVIVAL RATE OF EGGS WHEN EXPOSED TO DIFFERENT AMOUNTS OF EVAPORATION AT DIFFERENT TEMPERATURES

The field experiment described in Section V showed that more of the young stages of *O. fasciculata* survived when the eggs had been placed under a dense cover of herbage. The most likely explanation for this result is that the dense cover provided more protection from desiccation. The laboratory experiments that are described in this section were done to test this hypothesis and especially to investigate the capacity of the eggs to survive exposure to dryness.

(a) Eggs at Different Stages of Development

Because little was known about the survival rate of eggs of *O. fasciculata* when exposed to dryness, the first experiment was planned as a guide for later work. Two temperatures were used (20.1 and 13.0°C) and eggs were exposed for 20 per cent. of their incubation period (3.0 days at 20.1°C and 6.75 days at 13.0°C). There were six levels of evaporation

at each temperature and saturation deficits were arranged so that, at any one level of evaporation, eggs were exposed to the same amount of evaporation at each of the two temperatures. That is, the product of saturation deficit (mm Hg) and length of exposure (days), a measure of the total evaporation, was the same. Air movement was constant at all the treatments, for the lids were not removed from the jars during the periods of exposure. The layout of the experiment is shown in Table 3.

There were 100 eggs for each treatment. Eggs were placed in scooped-out recesses in disks of plaster and the disks were placed in air-tight glass jars which were then placed in incubators. Atmospheric humidity in the jars was controlled by means of sulphuric acid solutions.

When their period of exposure was finished, eggs were removed from the jars and placed on moist filter paper in Petri dishes, and the dishes were placed in incubators at the same temperature as that used when the eggs were exposed to evaporation. This experiment was done three times, using eggs that had completed a third, a half, and three-quarters of their development (stages I, II, and III) respectively.

A record was kept of the emergence of larvae and proportions were transformed to degrees; the data are summarized in Table 3. The analysis of variance showed that there were no significant differences between the survival rates of eggs at the two temperatures or at the six levels of evaporation. However, differences between stages of development were highly significant ($P < 0.001$); the analysis of means (Table 3) shows that very few larvae emerged from eggs that were exposed to higher levels of evaporation after they had completed most of their embryonic development. The percentage emergence of larvae that were exposed when three-quarters of their development was completed (stage III, see Table 3) was 49.8, compared with 75.6 per cent. emergence for eggs that were exposed when one-half developed (stage II), and 77.5 per cent. for eggs exposed when one-third developed (stage I). Stages I and II differed significantly only at the higher temperature, and this increase in death rate, in addition to the very great increase in death rate at stage III, indicates that the ability of the egg to survive desiccation decreases as the embryo develops.

Failure to obtain significant differences between survival rates at the six levels of evaporation suggested that the amount of evaporation was not severe enough at the drier levels. In subsequent experiments this treatment was made more severe.

A second experiment (2A) was similar to the preceding one and was designed to elaborate the information already obtained. There were two temperatures (16.9 and 13.4°C) and at each were six levels of evaporation together with a level where eggs were in a nearly saturated atmosphere. Compared with the previous experiment, the period of exposure was increased from 20 per cent. to 48 per cent. of the incubation

period of the eggs at each temperature (9.1 days at 16.9°C and 14.9 days at 13.4°C) and the air was drier. The same method was used in which the total evaporation was the same at any one level of evaporation at the

TABLE 3

DESIGN OF EVAPORATION EXPERIMENT AND PERCENTAGES OF LARVAE THAT EMERGED FROM
EGGS AT DIFFERENT STAGES OF THEIR DEVELOPMENT

(a) *Design of Laboratory Experiment, 1952*

Temp. (°C)	Length of Exposure to Evaporation (days)	Saturation Deficit (mm Hg) Levels of Evaporation					
		1	2	3	4	5	6
20.1	3.00	1.50	3.00	3.75	4.50	5.25	6.75
13.0	6.75	0.67	1.34	1.67	2.00	2.33	3.00

(b) *Transformed Percentages (in degrees) of Larvae that Emerged from Eggs Exposed to Evaporation*

Stage	Temp. (°C)	Levels of Evaporation						Totals all Levels
		1	2	3	4	5	6	
I	20.1	65.65	64.90	66.42	62.72	75.82	68.87	404.38
II		58.69	61.34	56.17	57.42	60.00	56.17	349.79
III		40.40	56.17	43.28	51.35	38.65	43.28	273.13
Total		164.74	182.41	165.87	171.49	174.47	168.32	1027.30
I	13.0	50.77	50.18	66.42	52.53	57.42	58.69	336.01
II		63.44	64.90	51.35	52.53	64.16	64.90	361.28
III		42.71	53.13	46.72	41.55	47.29	33.83	265.23
Total		156.92	168.21	164.49	146.61	168.87	157.42	962.52
I	Totals for	116.42	115.08	132.84	115.25	133.24	127.56	740.39
II	both	122.13	126.24	107.52	109.95	124.16	121.07	711.07
III	temperatures	83.11	109.30	90.00	92.90	85.94	77.11	538.36
Grand totals		321.66	350.62	330.36	318.10	343.34	325.74	1989.82

(c) *Analysis of Means: Temperature and Egg Stage*

Temp. (°C)	Egg Stage			Minimum Difference for Significance at $P<$		
	I	II	III	0.05	0.01	0.001
20.1	67.40	58.30	45.52	6.59	9.36	13.55
13.0	56.00	60.21	44.21			
Means	61.70	59.26	44.86			

two temperatures. The experiment started when the eggs had completed 8 per cent. of their embryonic development.

Each treatment contained four groups of 25 eggs and each group was in a wire-gauze basket (eggs were spread evenly over the bottom

of the basket) resting in an air-tight jar. Atmospheric humidity inside the jars was controlled with sulphuric acid solutions. For the control treatments the baskets rested on moist filter paper in jars containing distilled water. At the end of treatment the eggs were placed on moist filter paper in Petri dishes and a record was kept of the numbers of larvae that emerged and of their incubation period.

It had been intended to record the weight of each egg before and after exposure to dryness but, because the eggs were so small (*c*. 0.09 mg for a turgid egg) and the torsion balance not sensitive enough, eggs had to be weighed in groups of 25. Each group was weighed before and after exposure and also after the eggs had been replaced on moist filter paper. The latter weighings were done to find if a partially desiccated egg was able, when placed on a moist surface, to regain the water that it had lost.

TABLE 4

SUM OF SQUARES OF VARIATES SELECTED FOR THE PARTIAL REGRESSIONS

Variate	Sum of Squares	Variate	Sum of Squares
x_1	0.7506	$x_1 Y_1$	-36.5950
x_2	2.5926	$x_2 Y_1$	-140.3320
x_3	0.6768	$x_3 Y_1$	-60.9923
x_4	54.9800	$x_4 Y_1$	-210.6364
$x_1 x_2$	0.4994	$x_1 Y_2$	1.4370
$x_1 x_3$	0.0483	$x_2 Y_2$	14.0256
$x_1 x_4$	-0.2400	$x_3 Y_2$	3.2467
$x_2 x_3$	1.0913	$x_4 Y_2$	291.6327
$x_2 x_4$	-0.4825	Y_1	14411.0073
$x_3 x_4$	-0.9076	Y_2	1693.6811
		$Y_1 Y_2$	-2305.6145

Separate analyses of variance were done on the initial weights and losses of weight of the groups. Some of the groups differed significantly in initial weight, despite the care taken to select them at random from a single large group of eggs. Loss of weight during the exposure to evaporation was closely associated with dryness; the drier the air, the greater was the loss of weight.

Analysis of the percentage emergence of larvae (data transformed to degrees) showed that the only significant differences between the means of levels of evaporation were between levels 3 and 4 and between 5 and 6. This was rather puzzling, because the mean losses of weight of the other groups differed significantly, i.e. the amount of water lost did not appear to be associated with survival rate. Also, temperature had an influence on survival rate (more larvae emerged at the higher temperature) but not on the amount of water that the eggs lost.

Because of the conflicting results of the three analyses of variance it was decided to test the data further by fitting them to a partial

regression in which Y_1 referred to the survival rate expressed in degrees and four independent variates were original weight (x_1), loss of weight (x_2), specific gravity of the acid solutions (x_3), and temperature (x_4). Specific gravities of the acid solutions were included to see whether the acid itself had any influence on the developing eggs, e.g. harmful effect of fuming. A second dependent variate, duration of incubation period in days (Y_2), was included so that the influence of the four independent variates on it could be examined. There were 55 observations and the sum of squares and products of the variates are given in Table 4.

The first analysis by partial regression showed that original weight and specific gravity of the acid solutions had no influence on survival rate, independently of loss of weight and temperature; so they were discarded. Results of the second partial regression of Y_1 on loss of weight and temperature are shown in Table 5. This partial regression was

TABLE 5

PARTIAL REGRESSION OF SURVIVAL RATE (IN DEGREES) ON LOSS OF WEIGHT (x_2) AND TEMPERATURE (x_4)

Variate	Regression Coefficient	Standard Error	t	$P<$
x_2	−54.92431	6.5620	8.370	0.001
x_4	−4.30861	1.4247	3.025	0.01

Analysis of Variance

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	Variance Ratio	$P<$
Regression	2	8615.1863	4307.5931	38.65	0.001
Residual	52	5795.8210	111.4581		
Total	54	14411.0073			

significant $(P < 0.001)$ and accounted for 58 per cent. of the variance of Y_1. With the more sensitive analysis by partial regression it was possible to demonstrate that the numbers of larvae that emerged at any one level of evaporation were closely associated with the amount of water lost from the eggs (independent of temperature). There was about a 6 per cent. decrease in survival rate for each 0.1 mg of weight lost by a group. Temperature also was closely related to survival rate and there was a 2.5 per cent. increase in survival for each °C increase in temperature, independent of loss of weight.

The first partial regression of duration of incubation period (Y_2) on the four independent variates showed that original weight (x_1) contributed practically nothing to the variance of Y_2 and so it was discarded. Results from the second analysis are shown in Table 6. This analysis shows that the regressions were very significant and accounted for 98 per cent. of the total variance of Y_2; only 2 per cent. of the variance of

the dependent variate could be attributed to "error". Temperature was clearly the most important independent variate and for each °C increase in temperature the incubation period decreased by 3 days. The amount of water lost by the eggs also had an influence on the speed of development; for each 0.1 mg lost by a group, the incubation period was increased by 1 hr. The reduction in speed of development associated with exposure to increasing amounts of evaporation probably was caused by the loss of water reducing the rate of metabolism of the eggs and so retarding development (Wigglesworth 1950).

TABLE 6

PARTIAL REGRESSION OF DURATION OF INCUBATION PERIOD (DAYS) ON x_2, x_3, AND x_4

Variate	Regression Coefficient	Standard Error	t	$P<$
x_2	4.11877	0.91829	4.485	0.001
x_3	5.45497	1.81615	3.004	0.01
x_4	5.42861	0.11429	47.499	0.001

Analysis of Variance

Source of Variation	Degrees of Freedom	Sum of Squares	$P<$
Regression	3	1658.6391	0.001
Residual	51	35.0420	
Total	54	1693.6811	

Two other experiments were done at the same time as the previous experiment (2A). One (expt. 2B) was done to find whether eggs from Kalangadoo differed from those from Mil Lel (used in experiment 2A) in their ability to survive dry conditions. There were not many eggs from Kalangadoo and only one temperature (16.9°C) was used. There were five levels of evaporation and a control level, and at each level were four groups of 25 eggs. The experiment started when the eggs were at the same stage of development as in experiment 2A, they were exposed for the same length of time as those at 16.9°C in that experiment, and were treated in the same way in every respect. In the third experiment (2C) eggs from Mil Lel were allowed to complete 45 per cent. of their development before they were exposed to dryness. Eggs for the different treatments were chosen at random from the same group of eggs that was used for experiment 2A. Thus, the results of this experiment may be compared with those of 2A, where the eggs had completed only 8 per cent. of their development when they were exposed to evaporation. Three temperatures (20.1, 16.9, and 13.4°C) were used, and there were four levels of evaporation and a control at each temperature. The total evaporation was the same at any one level at each of the temperatures. Each treatment contained four

TABLE 7
COMBINED PROBIT ANALYSIS FOR LABORATORY EXPERIMENTS 2A, 2B, AND 2C

Experiment 2A						Experiment 2B			Experiment 2C								
Temp. 13.4°C			Temp. 16.9°C			Temp. 16.9°C			Temp. 13.4°C			Temp. 16.9°C			Temp. 20.1°C		
	Death Rate			Death Rate			Death Rate			Death Rate			Death Rate			Death Rate	
Evapn.*	(%)	Probit	Evapn.	(%)	Probit	Evapn.	(%)	Probit	Evapn.	(%)	Probit	Evapn.	(%)	Probit	Evapn.	(%)	Probit
83.26	78	5.77	80.90	85	6.04	90.14	70	5.52	82.68	96	6.75	60.32	67	5.44	61.16	100	∞
71.91	45	4.87	69.34	29	4.45	85.52	83	5.95	72.83	71	5.55	45.85	18	4.08	45.44	92	6.41
60.55	28	4.42	57.78	17	4.05	78.59	35	4.61	61.02	51	5.05	33.78	2	2.95	34.08	39	4.72
45.42	2	2.95	46.23	7	3.52	64.72	27	4.39	45.28	9	3.66						
34.06	1	2.67	34.67	4	3.25	60.10	17	4.05									
22.71	5	3.36															

Regression coefficient (b): 0.0704 ± 0.0063 (for all temperatures except 20.1°C) 0.1476 ± 0.0213

LD_{50}: 74.5176 ± 1.2117 (expts. 2A and 2B) 59.9986 ± 1.4716 (expt. 2C, 13.4° and 16.9°C) 35.97 ± 0.806 (expt. 2C, 20.1°C)

Analysis of χ² for Test of Parallelism

	D.F.	S.S.	M.S.	P<
Parallelism of regressions	4	8.7106	2.1777	n.s.
Residual heterogeneity	13	39.7618	3.0586	0.001
Total	17	48.4724		

Fiducial Limits

Differences between Experiments:	Mean	P<
2A 16.9° and 2B 16.9°C	6.3260 ± 3.0085	n.s.
2A 16.9° + 2B 16.9° and 2A 13.4°C	3.6916 ± 2.6432	n.s.
2A 13.4° and 2C 13.4°C	9.6140 ± 2.9472	0.05
2A 16.9° + 2B 16.9° and 2C 16.9°C	18.9893 ± 2.7759	0.05
2C 13.4° and 2C 16.9°C	5.6837 ± 3.1916	n.s.
2A 13.4° + 2A 16.9° + 2B 16.9° and 2C 13.4° + 2C 16.9°C	14.5190 ± 1.9059	0.05

* As indicated by the product of saturation deficit (in mm Hg) and length of exposure (days).

groups of 25 eggs; the same method of exposure was used as in experiment 2A.

The three experiments were analysed separately by probit analysis. Data from each of the six treatments were then taken in pairs and estimates of LD_{50} and regression coefficients (b) were compared. These tests of parallelism showed that it would be permissible to do a single analysis of all the data except those from 20.1°C of experiment 2C (see Finney 1947, Ch. 5). With the single analysis it was possible to compare
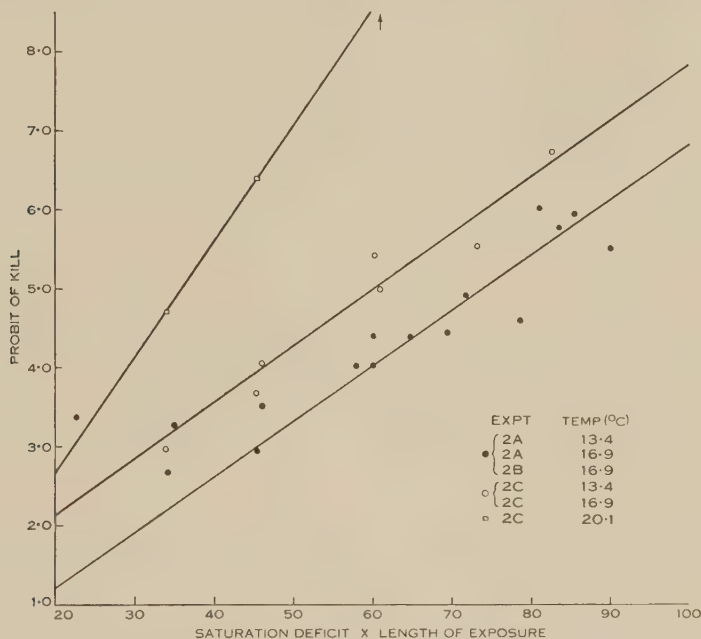

Fig. 2.—Probit regression lines showing relationship between probit of kill and amount of evaporation to which eggs of O. fasciculata were exposed.

the ability of eggs in different stages of development and from different places to survive at a given level of evaporation, and also to compare their response to the loss of small and large amounts of water; in other words, to see if there were significant differences between the values for LD_{50} or the regression coefficients.

Results of the combined probit analysis are given in Table 7 and the probit regression lines are shown in Figure 2. The test of parallelism showed that the regression coefficient was the same for each temperature. This value was small, indicating a rather wide range between the amount of evaporation needed to kill a few eggs and that needed to kill most of them. The positions of the 13.4 and 16.9°C lines for experiment 2A, and the 16.9°C line for experiment 2B, in relation to the ability of the eggs to survive loss of water, did not differ and so only one line was needed

for the three treatments (see Fig. 2). Although the regression coefficient for the 13.4 and 16.9°C treatments for experiment 2C was the same as for the previous three treatments, the eggs were more susceptible to dryness and the value for LD_{50} differed significantly from that for the other treatments. However, the values for LD_{50} of these two treatments did not differ between themselves and the one regression line shows the relationship between exposure and the probit of kill.

The positions of the three regression lines show that eggs that had completed 8 per cent. of their embryogenesis (whether from Mil Lel or Kalangadoo) were much more resistant to evaporation than were eggs that had completed 45 per cent. of their development. However, the relative lethal influence of short and long exposures to dryness was the same and so the lines are parallel. A separate analysis showed that eggs at 20.1°C (expt. 2C) differed in their response to short and long exposures and were more susceptible to dryness, so the regression line for this temperature has a lower value of LD_{50} and a steeper slope than the others.

(b) *Survival Rate when Different Proportions of Water are Lost*

The experiments described in Section III(a) showed that as the exposure to evaporation was increased fewer eggs survived, and that survival rate was associated with the stage of embryonic development of the eggs. The experiment to be described here was done to determine the relationship between the proportion of water lost by the eggs and their survival rate.

Ten groups of 200 eggs were selected at random from eggs that had completed 15 per cent. of their embryogenesis. One group was weighed and then oven dried to obtain the moisture content; this was 61.6 per cent. of the total weight of the eggs. Eight of the remaining groups were weighed and placed in individual wire-gauze baskets in a desiccator in which the air was maintained at a relative humidity of 65 per cent. and the desiccator was placed in an incubator at 13.4°C. This combination of relative humidity and temperature gave a saturation deficit of 4.06 mm Hg. The remaining group of eggs was weighed and put in a basket resting in an air-tight jar containing water. Having the original weights of the groups, and an estimate of the amount of water in each, it was possible to determine how much weight any one group should lose to correspond to a given proportion of its original water.

It was not known how much water the eggs could lose without damaging the developing embryos but from the work done on the eggs of other insects it was expected that few larvae would emerge from eggs that had lost half their water; the amount of water lost from eggs in this experiment ranged from 7 to 50 per cent. of their original water. The method used was to weigh the groups at intervals and when the eggs in any one group had lost a certain proportion of their water they were

placed on moist filter paper in a Petri dish and the dish was returned to 13.4°C.

Eggs used in this experiment were from Mil Lel, and the same sort of experiment was also done with eggs from Kalangadoo; five groups of 100 eggs were exposed to water loss ranging from 35.5 to 61.5 per cent. of their water content before desiccation, one group was kept in nearly saturated air, and one group was oven dried. Eggs were at the same stage of development as in the previous experiment, and the same temperature and method of exposure were used.

TABLE 8

COMBINED PROBIT ANALYSIS FOR LABORATORY EXPERIMENT ON INFLUENCE OF PROPORTION OF WATER LOST ON SURVIVAL RATE OF EGGS

Eggs from Mil Lel			Eggs from Kalangadoo		
Water Lost (%)	Death Rate		Water Lost (%)	Death Rate	
	(%)	Probit		(%)	Probit
50	64	5.36	61.5	88	6.18
45	61	5.28	47.5	84	5.99
35	27	4.39	39.5	29	4.45
30	19	4.12	35.5	14	3.92
25	8	3.59			
20	6	3.44			
10	4	3.25			
7	5	3.36			

Regression coefficient (b) 0.0692 ± 0.0091
LD_{50}* 43.1980 ± 0.9834

Analysis of χ^2 for Test of Parallelism

	Degrees of Freedom	Sum of Squares	Mean Square	$P<$
Parallelism of regressions	1	6.5928	6.5928	n.s.
Residual heterogeneity	8	43.3445	5.4181	0.001
Total	9	49.9373		

* Difference between LD_{50} for eggs from Mil Lel and Kalangadoo = 0.9898 $\pm$ 0.9834 (n.s.).

The numbers of larvae that emerged from each group of eggs were recorded and data from the two experiments were analysed separately by probit analysis. Values for LD_{50} and b were almost the same and so a combined probit analysis was done. Results are given in Table 8 and the probit regression line is shown in Figure 3. A 43 per cent. loss of water resulted in a 50 per cent. mortality and the small value for b shows that there was a rather wide range between the level where few larvae emerged and where most emerged.

(c) Eggs that Lost Water at Different Rates

This experiment was designed to study the survival rate of eggs when exposed to the same amount of evaporation but when the rate at which
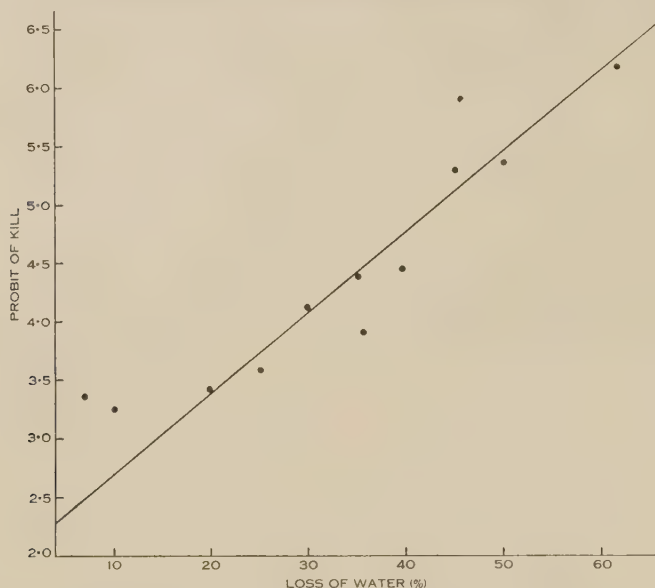

Fig. 3.—Probit regression line showing relationship between probit of kill and the proportion of water lost by the eggs of *O. fasciculata*.

water was lost from the eggs differed. This was done by exposing the eggs to seven different saturation deficiencies for different times which

TABLE 9

INFLUENCE OF RATE OF EVAPORATION ON SURVIVAL RATE OF THE EGGS

Level of Dryness (in the order of rate of evaporation)	Saturation Deficit (mm Hg)	Relative Humidity (%)	Length of Exposure (days)	Mean Emergence (percentage emergence transformed to degrees)	Minimum Difference for Significance at $P<$ 0.05 0.01 0.001
0	—	100	33	76.8	5.05 6.84 9.17
1	2.29	80	32	65.1	
2	2.79	77	26	54.2	
3	3.56	70	20	48.3	
4	4.06	64	18	40.7	
5	5.08	56	14	42.9	
6	8.89	22	8	21.1	
7	10.41	8	7	26.4	

were chosen such that the product of saturation deficit and time was nearly constant. One lot of eggs was kept at nearly 100 per cent. relative

humidity. Four groups of 25 eggs were kept at each rate and all were at 13.4°C. The seven rates of evaporation with their lengths of exposure and other data are given in Table 9.

Eggs were placed in baskets over sulphuric acid solutions in air-tight jars and after treatment were removed and placed on moist filter paper. The eggs had completed 15 per cent. of their development at the beginning of the experiment.

A record was kept of the numbers of larvae that emerged from each group and the mean emergence (in degrees) is given in Table 9. An analysis of the data showed that the rate of evaporation had a significant influence on the numbers of larvae that emerged ($P < 0.001$), even though the amount of evaporation was practically the same at rates 1-7. As the rate of evaporation increased fewer larvae emerged. The only inconsistencies were between the mean survival rates of levels 4 and 5, which did not differ significantly, and of levels 6 and 7, where more larvae emerged at the higher rate of evaporation (just significant at $P = 0.05$).

VII. Discussion

The speed of development of eggs of *O. fasciculata* at constant temperatures is quite different from that of *O. intricata* Walker in Tasmania. At 21.2°C and on moist paper, the mean incubation period of *O. fasciculata* eggs was 13 days while *O. intricata* eggs at the same temperature and level of moisture took 63 days; at 24°C the former eggs took 11 days to hatch and the latter 71 days (data for eggs of *O. intricata* are from an unpublished report by Mr. Martyn, Tasmanian Department of Agriculture). The differences in speed of development appear to be related to the date when the eggs are laid and may be regarded as adaptations by which the two species are able to survive the dry summer. Eggs of *O. fasciculata* are laid early in the spring and the larvae hatch and become established in burrows before the summer. If their speed of development were the same as *O. intricata*, larvae would appear in early summer and would be more exposed to unfavourable weather than older larvae. On the other hand, eggs of *O. intricata* are laid during mid to late summer and the larvae do not hatch until mid autumn; with a more rapid development larvae would appear during late summer, when the weather would be more severe.

Results of the field experiment described in this paper showed that the sort of place where the eggs were laid had an important influence on their survival rate. An unimproved pasture may be considered as unfavourable for the species because there is not sufficient surface cover to protect the eggs and young larvae against loss of water. But an improved pasture (because it carries a dense growth of grasses and clover) provides more shelter for the young stages and therefore is likely to favour a higher survival rate. However, the removal of cover from an improved pasture just before or during the early part of the period when

eggs and young larvae are present (September-November) may make this situation unfavourable; the proper timing of cutting herbage for hay (and the prompt removal of the cuttings) or heavy grazing by sheep may be expected to make an area less favourable for *O. fasciculata* during this critical stage in its life-cycle.

The analysis of the field experiment described in Section V showed that there was no significant difference between the survival rates where there were 50 eggs per sq. yd and 1000 per sq. yd, i.e. the same proportion survived at the higher density as at the lower. However, with the split-plot design of the experiment the egg densities were not compared so accurately as the method of application or type of cover because there was less replication and the method of application and type of cover differences were included in the error for evaluating density effects.

Contrary to expectation, there was a higher survival rate when eggs were scattered than when they were grouped. This was unexpected because the female lays most of her eggs in groups. After mating, the female crawls under the herbage and comes to rest on the surface of the ground. After fluttering about briefly she settles down and starts to oviposit; most of the eggs are then laid. The higher survival rate of scattered eggs in this experiment suggests that it is not to the advantage of the species, living as it does today in improved pastures, to lay eggs in groups. It is not known what additional hazards beset a larva that is living as one of a group. Under natural conditions, emerging larvae establish themselves in colonies under silken webbing among surface debris and live in these colonies for several weeks before constructing individual vertical burrows in the soil. The silken webbing should provide additional protection for the larvae, but, on the other hand, cannibalism may reduce their numbers. No evidence of cannibalism among young larvae was found in the laboratory but this does not mean that it does not occur in the field.

It may be that laying eggs in large clumps was an adaptation which resulted in a higher survival rate in native pastures. This could be so, because these pastures are composed mainly of grasses having a tussocky growth and there is a great deal of bare ground between the tussocks. After mating, the female would crawl under a tussock to seek shelter and would lay her eggs there. If eggs had been scattered over the ground most would have come to rest in unfavourable situations. Today, however, improved pastures provide large areas of favourable cover and it would be expected that eggs scattered over such an area would have a good chance to survive, but the species seems not yet to have become adapted to this change in its environment. Native pastures have been replaced by improved pastures mainly during the last 30 years.

Eggs that are not in contact with free water may be expected to lose water and it is likely that eggs located under a mat of herbage stand less chance of losing water than eggs in no such protected situation.

In the experiment done to study the influence of the rate of water loss on survival rate, most larvae emerged from eggs that were at a moist level for a long time, and as the rate of evaporation increased fewer larvae emerged, although all groups were exposed to the same amount of evaporation. However, it is not possible from this experiment to say precisely what caused fewer larvae to emerge as the rate of evaporation increased. This could have been (1) damage to the developing embryos; (2) eggs at the driest level were exposed for a small proportion of their embryonic period while eggs at the wettest level were exposed for a large proportion and the difference in the stages of development might have had an influence on survival rate; (3) as the air became drier the cuticle of the eggs may have changed in texture so that even healthy larvae could not break through.

In all of the experiments where groups of eggs were weighed, there was no evidence that the eggs were able to replace water lost during exposure to evaporation. A few groups out of a total of 155 used in the experiments increased very slightly in weight and it was thought that in these few cases not all of the external water had been removed from the eggs before they were weighed.

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THE ECOLOGY OF *ONCOPERA FASCICULATA* (WALKER) (LEPIDOPTERA: HEPIALIDAE) IN SOUTH AUSTRALIA

III. THE INFLUENCE OF TEMPERATURE AND MOISTURE ON SURVIVAL RATE OF THE LARVAE

By P. E. MADGE*

Summary

In South Australia the underground grass caterpillar, *Oncopera fasciculata* (Walker), is found only in the higher rainfall area in the south-eastern portion of the State. It appears that the distribution and numbers of this pest of improved pastures are mainly restricted by unfavourable weather (dry and hot) during the egg and early larval stages (late spring–early summer). These stages, as well as older larvae established in subterranean burrows, stand a better chance to survive the dryness and heat where the surface of the ground is covered with dense herbage. Unfed, first-instar larvae are much more susceptible to loss of water than are the eggs.

Larvae remain virtually dormant during the summer, but from about April onwards they grow rapidly. The resumption of active feeding and growth is associated with the first substantial autumn rains. During autumn, when the rainfall may be intermittent, the larvae feed more actively during wet periods and become relatively inactive again during dry periods.

The relative humidity of the air at the base of a subterranean burrow where the larvae lives was usually above 95 per cent., even when the relative humidity of the air just above the mouth of the burrow was as low as 65 per cent. No measurements were taken during the height of the summer, when the burrows may have been drier than this.

I. INTRODUCTION

Larvae of *Oncopera fasciculata* (Walker) appear in late spring and after 2-3 weeks on the surface of the ground each constructs a subterranean burrow; the feeding stage lasts until midwinter. While on the surface of the ground larvae are often found under a communal mat of webbing. Apart from the scant protection afforded by this webbing, the extent to which they may be exposed to dryness and heat may depend largely on the quantity and type of herbage and surface debris.

The subterranean burrow is covered with a silken cap which should provide some protection against unfavourable weather. From early summer until the end of the feeding stage the burrow is increased in depth, providing the larva with increased protection. But, from the time burrowing starts until early summer, the larva is within 1 in. of the surface and may be exposed to excessive dryness or heat.

* Waite Agricultural Research Institute, University of Adelaide; present address: Department of Zoology, University of Adelaide.

Two quite elaborate field experiments were done during 1951 and 1952 to measure the influence of surface cover on the survival rate among larvae established in subterranean burrows. The results, however, were not striking enough to justify reporting them in detail. The weather during both of these summers was dry and death rates in all of the treatments varied from 89 per cent. to 94.5 per cent. The survival rate was not influenced by the initial density of the population which varied from 50 to 600 eggs per sq. yd. The survival rate on plots that carried

TABLE 1

COMBINED PROBIT ANALYSIS OF DATA FROM LABORATORY EXPERIMENT ON UNFED, FIRST INSTAR LARVAE

Temp. 16.9°C				Temp. 20.2°C		
Evaporation*	Death Rate		Evaporation	Death Rate		
	(%)	Probit			(%)	Probit
12.17	93	6.48	16.29		100	∞
9.24	57	5.18	12.10		95	6.64
6.81	45	4.87	9.08		70	5.52
4.63	—	—	6.04		47	4.92

Regression coefficient (b) 0.2825 ± 0.0399
LD_{50}† 7.1324 ± 0.5326

Analysis of χ^2 for Test of Parallelism

	Degrees of Freedom	Sum of Squares	P
Parallelism of regressions	1	0.003	n.s.
Residual heterogeneity	3	3.495	n.s.
Total	4	3.498	

* As indicated by product of saturation deficit (mm Hg) and length of exposure (days).

† Difference between LD_{50} for 16.9 and 20.2°C $= 1.0913 \pm 0.6729$ (n.s.).

the naturally dense herbage was 11 per cent., compared with 5 per cent. on plots where the herbage had been mown close to the ground. This difference was significant at $0.01 < P < 0.02$. Although these experiments had shown that the amount of surface cover influenced the survival rate of larvae, this influence was small relative to the overall influence of the dry weather.

It was not practicable to study the survival rate of newly hatched larvae in the field but this paper reports the results of an experiment done in the laboratory with larvae in this stage of their development. This paper also describes field experiments on the moisture requirements of larvae established in individual subterranean burrows; and the humidity within the burrow of the larva has been measured.

—   P. E. MADGE

II. Survival Rate of Unfed, First Instar Larvae when Exposed to Different Amounts of Evaporation

Two temperatures were used in this experiment (16.9 and 20.2°C) and at each were four levels of evaporation, measured in units of saturation deficit (in mm Hg) × length of exposure (days), together with a treatment where larvae were kept in a nearly saturated atmosphere. There were 50 larvae at each treatment and each larva was in an individual "Cellophane" tube. The tubes were placed in a wire-mesh basket resting in an air-tight jar in which the humidity was controlled with sulphuric acid solutions or distilled water.
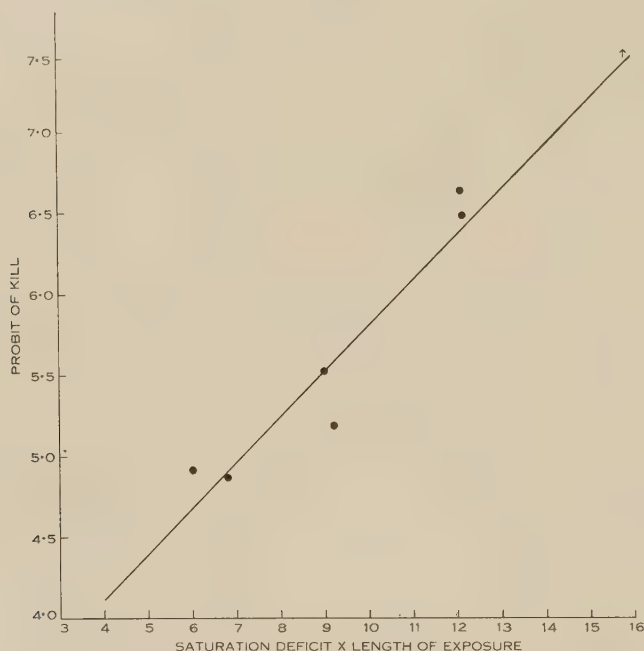
Fig. 1.—Probit regression line showing the relationship between exposure to evaporation and probit of kill.

Larvae were examined at intervals, and, when it appeared that about half the larvae had died at the mid level of evaporation at each temperature, all the larvae were removed from that temperature and placed in a moist environment at the same temperature in which they had been exposed. It was then possible to obtain counts of the numbers of larvae that did not survive at each treatment.

Separate probit analyses of data for the two temperatures showed that the slopes of the regression lines were almost the same, as were values for LD$_{50}$, and so a combined probit analysis was done (Finney 1947). Results of this analysis are given in Table 1 and the probit regression line is shown in Figure 1. The lines were parallel and the

value of the regression coefficient was large, showing that there was a rather narrow range between the exposure where few larvae were killed and that where most were killed at each temperature.

III. Influence of Moisture and Type of Food on Growth and Activity of Larvae

Although larvae may be found in the field from about October to July, field observations suggest that for much of this time they are relatively inactive. From the time the larva becomes established in its burrow (about November) until about April, there is a slow, steady increase in size and a corresponding increase in the depth and width of the burrow, but the growth during this, the warmest part of the year, is very little compared to the rapid growth from about April onwards, when the temperature is much lower. This very great increase in the size of the larva appears to be related to the first substantial autumn rains. At this time several important changes occur in the environment of the larva. The soil becomes moist and this in turn causes a rapid germination and growth of annual grasses and clovers, providing green feed. Also, the air becomes more humid and as autumn progresses the temperature falls and the days become shorter. It is not known exactly how these changes stimulate the larvae to greater activity, or which changes are more important, but the experiments described below throw some light on this problem.

A series of field experiments was done during the autumn of 1954 to study the influence of moisture and food on the growth and activity of larvae of *O. fasciculata*. This work was done in the autumn so that larvae would be easy to find in the field and large enough to handle without difficulty. Twenty larvae were used for each treatment and each larva was placed in a "Cellophane" container, weighed on a torsion balance (to 0.01 mg), and the container was then placed on a hook in the lid of an air-tight glass jar containing a sulphuric acid solution. Earlier tests showed that an exposure to evaporation of about 4 hr was needed to reduce the weight of a larva by about 20 per cent., and that the larva was able to recover after having lost this amount of water. Air inside the glass jar was circulated by pumping a rubber syringe attached to the lid of the jar as soon as larvae were placed in it and at regular intervals afterwards. After this exposure, each larva was reweighed, together with its faeces. Larvae were then removed from their "Cellophane" containers and placed in vertical holes in the ground which were the same depth and diameter as natural burrows. The location of each larva was recorded and the group of larvae then received one of the treatments to be described later. After one or two nights in the "burrows", larvae were removed, placed in individual "Cellophane" containers, and weighed; this last weighing showed whether the larvae had lost or gained weight during the time they were in the "burrows" and exposed to a particular treatment.

Thirteen groups of larvae were treated during a period of about 3 weeks but the only ones to be discussed in detail here are the eight groups in which significant results were obtained. Heavy rains fell during the latter part of this work and so it was possible to compare the activity and growth of larvae before and after this "break" of the season. The treatments were done on a well-drained terra rossa soil at Mil Lel and on a low-lying meadow podsol north-west of Kalangadoo. A record of temperature and relative humidity during these studies was obtained from a thermohygrograph placed in the paddock alongside the treatment areas.

(a) *Before Break of the Season*

(i) *Treatment* 1: *Preliminary Weighings* (*Mil Lel*).—Because larvae were removed from burrows and, after exposure to dryness, were placed in artificial "burrows", there was a certain amount of silk-spinning activity while the larvae re-established themselves. Treatment 1 was done to obtain an estimate of how much weight larvae lost because of this disturbance so that a "correction factor" could be applied to the other treatments. Twenty larvae were dug up, weighed, and replaced immediately in individual "burrows" in the soil, from which surface growth had been removed. A leaflet of subterranean clover (*Trifolium subterraneum* L.) was placed over the entrance of each "burrow" to provide food for the larvae so they would not leave their "burrows". A double thickness of hessian bags was then placed over the area. Forty-eight hr later the bags were removed, the amount of clover leaflet eaten by each larva recorded, and the larvae were dug up and weighed; three larvae had left their "burrows" and so were discarded.

After adjustments were made for the amount of food eaten by each larva, a *t*-test was done to determine the significance of the mean change in weight of the group. Table 2, which includes pertinent data of the eight treatments to be discussed, shows that larvae lost, on the average, 8.1 per cent. of their weight during the 48 hr in the "burrows"; this was clearly a significant loss and must be attributed largely to the activity of larvae in establishing themselves in the new "burrows".

The results were used as a correction for the results of later experiments. The mean loss of weight associated with establishing new "burrows" was subtracted from the gross loss or gain of weight determined in the later experiments and the variance was added to the variance of the other treatments.

The two nights that larvae were in "burrows" were mild (lowest temperature recorded was 16.5°C) and without rain but there had been a heavy dew. The bags prevented the deposition of dew near openings to the "burrows"; the soil was damp but there was no evidence of free water on the area when the bags were lifted.

(ii) *Treatment 2: Change in Weight when No Green Feed or Free Water Available* (*Mil Lel*).—Larvae in this group were placed in "burrows" which were covered with a layer of straw and bags. The straw was used to prevent too much surface movement of the larvae and the bags were to prevent any dew which might form from becoming available to the larvae. Under these conditions the only moisture available to the larvae was atmospheric or in the straw. Larvae were placed in "burrows"

TABLE 2

DATA FROM FIELD EXPERIMENT ON THE INFLUENCE OF MOISTURE AND FOOD ON GROWTH AND ACTIVITY OF THE LARVA

Treatment No.	Treatment	No. of Larvae	$\overline{x}$ (% loss or gain in weight)	$\Sigma(x-\overline{x})^2$	$\dfrac{s^2}{n}$	t	P
1	Control; not desiccated	17	−8.10	1079.85	3.97	4.07	0.001
2	Desiccated; no green feed or water	14	−9.25	735.85	8.01	3.27	0.01
3	Desiccated; green feed but no water	15	−10.85	463.23	6.18	4.36	0.001
		16	−6.59	1282.16	9.31	2.16	0.05
4	Desiccated; green feed and water	6	22.74	506.54	20.85	4.97	0.01
5	Desiccated; no green feed but water	15	14.25	847.41	8.00	5.04	0.001
6	Desiccated; no green feed but water	10	10.97	434.78	8.80	3.70	0.01
7	Desiccated; green feed and water	16	7.54	1073.93	8.44	2.60	0.02

one afternoon and were dug up the following morning; six were lost during the treatment. The remaining larvae had lost further weight; the mean loss was equivalent to 9.25 per cent. of their weight before being placed in the "burrows", and this loss was significant. The night when this group was exposed was cool and windy; the lowest temperature reading was 11°C, the highest relative humidity reading was 88 per cent., and no dew fell. Under these conditions larvae continued to lose weight while in the "burrows".

This treatment was repeated at Kalangadoo and larvae were left for two nights instead of one; here also they lost weight while in the "burrows" but the mean loss, 3.0 per cent. of their weight before treatment, was not significant ($P = 0.2$). There were fog and heavy dews during the treatment.

Although the Kalangadoo treatment was inconclusive, larvae did continue to lose weight, and this, together with the significant results from Mil Lel, suggests that larvae of *O. fasciculata* probably cannot absorb water from vapour in the air, as do some insects (Wigglesworth 1948), and, more important, during dry periods when no green feed is available, larvae may run the risk of using up their reserves of moisture if they are too active.

(iii) *Treatment 3: Change in Weight when Green Feed but No Free Water Available (Mil Lel and Kalangadoo).*—Larvae in these groups received no moisture in the form of free water but were given green herbage to eat. After the exposure to dryness, larvae were placed in "burrows" in the soil, the entrances were covered with freshly cut subterranean clover and Wimmera ryegrass (*Lolium rigidum* Gaud.), and the area covered with bags. Of the 20 larvae which were dug up at Mil Lel, three escaped from their "Cellophane" cages and two were lost from their "burrows". The larvae were left overnight in their "burrows" and were dug up and weighed the following morning. Although fresh green feed had been available, larvae lost an average of 10.85 per cent. of their weight during the treatment, and this loss was significant. It appears that green feed alone is not sufficient to cause greater activity and feeding among the larvae. The night when larvae were in "burrows" was mild (minimum temperature 13°C) and a slight amount of rain fell but it did not penetrate the bags and so would not have been available to the larvae.

The treatment just described was repeated at Kalangadoo. This group was left for two nights before being dug up and weighed. Here, also, larvae lost weight, even though fresh, green feed had been available; the grass and clover were still moist and green at the end of the treatment. During the time in the "burrows" larvae lost an average of 6.59 per cent. of their weight, and this was significant. Heavy dew formed on each of the nights that the larvae were in "burrows" but it did not penetrate the bags; the nights were cool and the lowest temperature recorded was 10°C. Results from this treatment were the same as at Mil Lel; when abundant green feed but no water was available—larvae continued to lose weight while in the "burrows".

(iv) *Treatment 4: Change in Weight when Green Feed and Free Water Available (Mil Lel).*—Because larvae in treatment 3 continued to lose weight even when green feed was available, the treatment was repeated here but the area containing larvae in "burrows" was not covered with bags so that they might have access to water in the form of rain or

dew. After the exposure to dryness, 15 larvae were placed in "burrows", green feed was provided, and the following morning nine were dug up and weighed; the mean weight of the larvae had not changed significantly during the time they were in the "burrows". The remaining six larvae were not dug up until the second morning and these had gained a significant amount of weight during their 48 hr in the "burrows"; the mean increase in weight was 22.74 per cent.

During the first night of exposure there was no rain or dew and weighings showed that the larvae did not change significantly in weight. During the second night a light rain fell and the remaining larvae gained significantly in weight. This result suggests that the moisture encouraged greater activity among the larvae and an uptake of food and water.

(v) *Treatment 5: Change in Weight when Straw and Free Water Available (Mil Lel).*—The results from treatment 4 showed that water appeared to have an influence on the activity and change in weight of *O. fasciculata* larvae. Therefore, in treatment 5, larvae were exposed to dryness in the jar, placed in "burrows", provided with a covering of straw, and then the treatment area was watered with a knapsack spray. Larvae were left in the "burrows" overnight and then were dug up and weighed; this weighing showed that when larvae were provided with moisture and straw from dead grass they increased significantly in weight; the mean increase was 14.25 per cent. It appeared that the presence of moisture caused the larvae to become more active and to drink and feed. The night that larvae were in the "burrows" was cold (minimum temperature was 6°C) and there was no rain or dew.

(b) After Break of the Season

The treatments described so far were done during early April, before any substantial amount of rain had fallen . The soil moisture at the surface was below the wilting point for herbage plants and although there had been some germination of subterranean clover in March this growth had wilted because there was no following rain. In mid April there was a heavy fall of rain (1.84 in. in 2 days) which caused a very rapid recovery of the herbage. Later in the year, when rainfall records were examined, the mid-April rains were recognized as the break of the 1954 season. The two treatments to be discussed now were done after the fall of rain, when the environment was very favourable for the larvae; the soil was moist and there was abundant green feed.

(i) *Treatment 6: Change in Weight when Straw and Free Water Available (Kalangadoo).*—After exposure to desiccation, 14 larvae were placed in "burrows" in the soil and the treatment area was covered with a layer of straw from dead grass. After a few showers of rain had fallen on the area it was covered with bags. Larvae were left overnight and dug up the following morning; four were lost during the digging. Each of the 10 larvae remaining had gained weight overnight; the mean was a

10.97 per cent. increase, and this was significant. The result was the same as in treatment 5, where the treatment area was watered with a knapsack spray. The moist conditions caused an increase in weight, and this increase probably was caused mainly by the uptake of water.

(ii) *Treatment* 7: *Change in Weight when Green Feed and Free Water Available* (*Mil Lel*).—Larvae were placed in "burrows" and the treatment area was covered with wet, green grass and clover, and then with bags. After 48 hr the 16 larvae remaining were dug up and weighed. All but two had gained weight during this treatment; the mean increase of 7.54 per cent. was significant. This result was the opposite of that obtained from treatment 3: with green feed only, larvae continued to lose weight, but with green feed and free water they increased significantly in weight.

Another group was set out in which larvae were placed in "burrows", given a treatment of green feed but no free water, and the treatment area was covered with bags. Larvae were dug up 48 hr later and weighings showed that their average weight had increased by 4.72 per cent.; this increase, however, was not significant $(0.1 < P < 0.2)$. There had been an overall gain in weight, as compared with a significant loss of weight when larvae received the same treatment before the rains.

IV. Studies on Relative Humidity within the Burrow of a Larva

At the same time as the experiments described in Section III, studies were made on the relative humidity within the burrow of an *O. fasciculata* larva. It was thought that the silken cap covering the entrance to the burrow, together with the moister soil beneath the surface of the ground, might result in air inside the burrows containing more moisture than air at the surface. The amount of moisture in the air was determined by inserting a piece of paper treated with cobalt thiocyanate (Solomon 1945). The technique used was to remove carefully the silken cap from a burrow, remove the larva, insert a strip of treated paper, and replace the cap. After a time the paper was removed, dipped in liquid paraffin wax to preserve the colour, and then an estimate of the relative humidity of the air obtained by comparing the colour of the paper with a series of standards. A larva was removed from its burrow by inserting a small piece of straw which the larva grasped in its mandibles thus enabling it to be lifted out. The time needed for the papers to reach equilibrium depended on the temperature and humidity of the air in the burrow, and in this work the paper strips were exposed for at least 30 min.

In order to obtain a comparison of moisture conditions in the burrow and on the surface of the ground, treated papers were placed in three situations for most of the observations—in the burrow (paper strips were 2 in. long), on the ground under herbage, and exposed on the surface. Tests were made near a thermohygrograph set out in the field and readings

were taken from it at the end of each period of exposure; these served as a check on the readings given by the papers in the "exposed" situation.

Results from a series of tests, given in Table 3, show that in all but three cases, readings obtained from treated papers exposed on the surface of the ground were very close to readings obtained from the thermo-hygrograph; figures from the former method were slightly lower than those from the latter. This close relationship shows that the treated papers gave a reliable indication of relative humidity.

TABLE 3

RESULTS FROM STUDIES WITH PAPERS TREATED WITH COBALT THIOCYANATE
Values are percentage relative humidity

Date	Time	Burrow*	Sheltered	Exposed	Thermohygro-graph
Mar. 31	5.45-6.45 p.m.	85-95	83	81	—
31	7.45-8.15 p.m.	88-92	92	88	90
Apr. 1	6.45-8.45 a.m.	85-92	65	58	69
1	10.45-11.30 a.m.	60-96	—	—	49
1	2.50-3.20 p.m.	55-97	—	—	44
2	11.15-11.45 a.m.	80-97	—	—	70
2	4.00-5.00 p.m.	83-97	82	72	78
3	7.15-8.00 a.m.	—	100	98	99
5	11.45-12.30 p.m.	90-97	65	53	54
9	1.15-2.45 p.m.	98-98	81	79	80
10	1.45-3.15 p.m.	88-98	78	65	68
11	1.15-2.00 p.m.	80-98	65	58	59
11	5.00-5.30 p.m.	95-98	87	83	74
12	2.15-3.00 p.m.	77-98	76	<50	42

* The first figure is the reading at the burrow entrance and the second figure is the reading near the bottom.

The driest air in the burrows was at the entrance and the wettest was at the bottom; there was a steady increase in moisture down the burrow. Burrows were slightly more than 2 in. long and larvae averaged 0.9 in. in length so that when in the lower inch of its burrow a larva would be surrounded by air nearly saturated with water vapour. Air under the herbage was drier than at the entrance to the burrows (except for the evening reading on March 31), although in some cases this difference was slight. As had been expected, air in exposed situations was drier than air under the herbage.

V. DISCUSSION

Results from the field experiments (mentioned in Section I) suggest that the sort of place where the later stages of larvae of O. *fasciculata* are living during summer has an influence on their chance to survive. As with the egg and young larva on the surface of the ground, a larva established

in a subterranean burrow seems to have a better chance to survive unfavourable weather (hot and dry) where the surface of the ground is covered with a mat of herbage.

Studies on the capacity of first instar larvae to survive exposure to dryness showed that these larvae were much more susceptible to loss of water than were the eggs. The median lethal dose for young eggs of O. *fasciculata* at 16.9°C was 74.5 (Madge 1956), while at the same temperature the median lethal dose for larvae was 7.1.

It was not possible to do laboratory experiments with later stages of the larvae because they are difficult to rear in the laboratory. Various techniques were tried but none was successful—most larvae died during the second ecdysis. Plots of herbage containing larvae were taken to the laboratory from the lower south-east of South Australia but in these cases most larvae died because there was no suitable way to protect them against the hot, dry weather in Adelaide during the summer.

It would appear from the experiments discussed in Section III that during the autumn, before substantial rains produce a growth of annual grasses and clovers, larvae of O. *fasciculata* remain relatively inactive, probably because of the hot, dry weather and the shortage of green feed. When they are disturbed and have to construct new burrows or webbing or both, a considerable amount of weight may be lost and, in this experiment, the loss was attributed mainly to silk-spinning. During a dry period it may not be to the advantage of larvae to feed, for such activity, when only dead growth is available, may cause a loss rather than a gain in weight. Even when green feed is available but the surface of the soil is dry and there is no free water, larvae may remain relatively inactive. However, after rain, or possibly heavy dew, larvae become active and do more feeding because of the moist conditions. This increased activity occurs not only when green feed is available but also when there is only dead growth.

The results from treatments 2 and 3 seem to indicate that feeding of O. *fasciculata* larvae is controlled by moisture and that they remain relatively inactive during dry periods. This is not surprising when it is noted that all 12 species of this genus in Australia are restricted to the wetter areas and probably are not adapted to living in dry situations. If O. *fasciculata* were so adapted, it might be expected that the larvae would behave as do some insects found in deserts, which obtain water by eating dead vegetation that has absorbed water from the atmosphere during the night (Buxton 1924). Or they might eat large amounts of food, much of which is excreted undigested, to obtain the water it contains. But O. *fasciculata* would seem to do none of these things. Larvae remain relatively inactive in their burrows during summer and become active only after the soil has been wetted. The species persists in the area where it is found because the autumn rains are relatively reliable.

The studies on moisture conditions inside the burrow of a larva showed that in the autumn a larva sheltering in the lower portion of its burrow is not exposed to the same degree of dryness as on the surface of the ground during a dry, hot day. However, the larva is likely to lose water when in the upper portion of the burrow or on one of its surface runways.

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A REVIEW OF THE AUSTRALIAN SPECIES OF *CYLINDROMYIA* MEIGEN AND *SARALBA* WALKER (TACHINIDAE: DIPTERA)

By S. J. PARAMONOV*

Summary

Ten new species of the genus *Cylindromyia* Meigen are described and information about the 11 species of this genus previously described has been greatly supplemented. A new key is also provided. This study has shown that the genus is extremely well represented in Australia and more species probably remain to be discovered in each State. Another genus of Cylindromiini, *Saralba* Walker, has been recorded for Australia for the first time, and one new species of it described.

INTRODUCTION

The present paper is the first attempt to revise the Australian species of *Cylindromyia* Meigen (*Ocyptera* olim.). Since Malloch's paper (1930)† dealing with this genus was published, much material has accumulated in the Australian museums. For this review the author has studied the material in the Division of Entomology Museum, C.S.I.R.O., Canberra, and in three Sydney collections. Ten new species are added to the 11 already described. It is quite evident that many species are as yet undescribed.

The structure of the claws and of the armature of the last sternal plate in the male, the presence or absence of long hairs and bristles on the legs, the form of the vein m_1, etc., are characters of use in differentiating the new species. Although these are superficially very similar to one another, morphological characters enable them to be readily distinguished.

Conclusions or generalizations cannot be drawn from the very limited material at present available.

The genus *Saralba* Walker is also discussed here on account of the superficial similarity of its species to certain common *Cylindromyia*. The two genera are not, however, closely related.

These flies may be important as parasites but studies of their life-cycles have only just begun; the present revision is regarded as a necessary preliminary to further studies on their biology and economic importance.

Genus CYLINDROMYIA Meigen

Cylindromyia Meigen, 1803, Illig. Mag. 2: 279.

Type species *Cylindromyia brassicaria* Fabr.

Elongated species of large to medium size; colour black, but abdomen

* Division of Entomology, C.S.I.R.O., Canberra, A.C.T.
† Malloch, J. R. (1930).—*Proc. Linn. Soc. N.S.W.* **55**: 312-16.

nearly always red except base, or except base and apex, or only at the sides. Head broader than thorax, convex behind, and much puffed out below. Frons somewhat broad, broadest in female, somewhat protruding. Jowls not broad, about one-fourth of the height of the eye. In both sexes small, more or less individualized ocellar bristles, and inner but no outer vertical bristles; in female 2 orbitals. Distinct postocellar and occipital bristles. Behind post ocular bristles no black hairs or only a few above. Frontal bristles only reaching to the insertion of antennae, in male all crossing, in female the uppermost directed forwards or more or less outwards. Cheeks bare. Vibrissae not ascending. Epistoma almost not retreating, with a low keel in the middle above, reflected and somewhat prominent below. Proboscis and oral cone rather long, of about equal length, the proboscis slender with small labella. Clypeus linear, only a little incised at apex. Palpi quite small and rudimentary. Antennae inserted at about the middle of the eye, somewhat short, 3rd joint from about as long to twice as long as 2nd; arista bare with 2nd joint a little or almost not elongated. Thorax rectangular; the transverse suture at or behind the middle. Three postsutural dorsocentrals, no acrostichals; a posthumeral and 2 intra-alar bristles. Scutellum with 1, 2, or 3 marginal bristles on each side as either the basal or both basal and apical may be wanting. Two sternopleural bristles. Pteropleura covered with short hairs, but without any bristle or bundle of longer hairs. Abdomen long, cylindrical or somewhat narrowing towards base; excavation at base small; either discal and marginal or only marginal bristles present; 2nd segment with bristles. Male genitalia forming a rounded knob at apex; 5th sternite small. Female abdomen ending with a thick or more slender ovipositor, curved in under venter, the last segment ending with 2 points or 2 larger claws. In some species there is in the female at the apical corners of the 2nd segment on ventral side a patch of strong short spinules, and a similar, but of less strong spinules, on 3rd segment. Legs long, with rather long bristles on ventral side of femora and on tibiae, but in female the femora nearly bare below, only hind femora with a bristle in the middle; the ventral bristle on middle tibiae present in both sexes. Claws and pulvilli strongly elongate in male. In female the 3 last joints on front tarsi dilated. Wings with 1st posterior cell closed and petiolate, the peduncle curved upwards, ending considerably before apex of wing; discal angle rectangular, without or with a short veinlet. No costal spine. The species are parasitic on imagines of *Rhynchota*.

KEY TO THE AUSTRALIAN SPECIES OF THE GENUS CYLINDROMYIA

1. Wings colourless or with weak coloration, at most only with the anterior half black. Abdomen usually with red or yellow markings 5
   Wings uniformly black or the colour concentrated along the veins also on the posterior half of wings. Abdomen black, without red markings 2
2. Base of abdomen with 2 lateral yellow transparent spots 3
   Abdomen black 4

3. Antennae yellow. Sides of 1st segment of abdomen with very large, yellow, transparent spot. At base of 1st segment of abdomen laterally, besides long hairs, there is present a strong bristle. Qld. ....*C. fenestrata*, sp. nov, ♂
    Antennae black. Sides of 1st segment of abdomen with a small, indistinct, transparent spot. At base of 1st segment of abdomen laterally, only long hairs. Lord Howe I. ....*C. howeana*, sp. nov, ♂, ♀

4. Wings of a very intense and uniform black, only area near posterior area sometimes slightly lighter. Body, including legs, antennae, and halteres, carbon black with silvery markings on head and thorax. Qld. ....
    ....*C. aterrima*, sp. nov, ♂
    Wings black but not very intensely so, the colour concentrated along the veins on the posterior half of the wings. Abdomen black. "Australia" ....
    ....*C. tristis* (Bigot), ♂

5. Wings hyaline or slightly darkened along the anterior margin. Centre of propleura bare 6
    Wings hyaline, but anterior third dark, sharply separated from the hyaline part. First posterior cell closed at very short distance before costa. Apical section of vein m_1 (4th longitudinal) nearly straight, its bend obtuse. Centre of propleura haired. N.S.W. ....*C. nigricosta* Malloch, ♂, ♀

6. Apical section of vein m_1 regularly and distinctly convex towards apex of wing; its bend regularly rounded 7
    Apical section of m_1 straight, or S-shaped or concave, never convex 8

7. Legs, humeral, and postalar calli and sides of thorax reddish yellow. W.A. ...
    ....*C. brunnea* Malloch, ♂
    Legs black, humeral, and postalar calli and sides of thorax black. N.S.W. ....
    ....*C. tricolor* Malloch, ♀

8. Black frontal stripe extremely narrow, about one-ninth of width of frons. A.C.T. ....*C. angustissimifrons*, sp. nov.
    Black frontal stripe always occupying distinctly more than one-ninth of width of frons 9

9. Femora and tibiae reddish 10*
    Femora and tibiae black 11

10. Antennae extremely long, reaching fully to the mouth edge. Bend of the vein m always with additional veinlet. N.S.W., Qld. ....*C. rufifemur*, sp. nov.
    Antennae short, not reaching the mouth edge. Bend of the vein m always rounded, without an additional veinlet ....*C. westralica*, sp. nov.

11. Abdomen wholly black, without reddish spots 12
    Abdomen always with reddish spots 15

12. Males 13
    Females 14

13. Length 7.5 mm. Only one specimen of male known. The species is not sufficiently described. N.S.W. ....*C. sydneyensis* Malloch, ♂†
    Length (probably) 5-6 mm (based on female size). The male of this species is unknown. N.S.W. ....*C. atratula* Malloch, ♂†

14. Genitalia furnished with a process on each side near base (see Fig. 1). Length 7.5 mm. N.S.W. ....*C. sydneyensis* Malloch, ♀
    Genitalia (see Fig. 2) without a process on each side near base. Length 5-6 mm. N.S.W. ....*C. atratula* Malloch, ♀

* See also the description of the enigmatical *O. diversa* Walker.

† The author has single males belonging to two different species of this group but he considers it advisable to wait until further specimens of both sexes are available, for neither appear to be specimens of *sydneyensis* or *atratula*.

15.   Third antennal joint oval, slightly longer than 2nd one, its apex slightly acute. India, Australia? ....*C. bicolor* (Bigot), ♀
       Third antennal joint distinctly longer than the 2nd one 16
16.   Vein m_1 forming a distinctly obtuse angle, the last portion of vein straight and having distinctly oblique position 17
       Vein m_1 forming at bend nearly a right angle, last portion of vein usually S-shaped and having a more vertical position 18
17.   Two last tergites predominantly reddish. Squamae alares white. Frontal stripe black, not parallel-sided, broadening towards ocelli. Tas. ....
       ....*C. hobartana*, sp. nov., ♂
       Two last tergites predominantly deep black, shining. Squamae alares yellow (possibly the colour is an artefact in the single specimen). Frontal stripe parallel-sided. N.S.W. ....*C. dayi*, sp. nov., ♂
18.   Males 19
       Females 21
19.   Inner and underside of hind femora in their basal part with very dense and long black hairs 20
       Inner and underside of hind femora only with short, sparse hairs. A.C.T., Qld., W.A. ....*C. unguiculata*, sp. nov., ♂
20.   Pollinosity of head and mesonotum predominantly golden. Fourth tergite always with reddish lateral triangles on anterior half. N.S.W., S.A., W.A. ....
       ....*C. flavifrons* Macquart, ♂
       Pollinosity of head and mesonotum predominantly silvery. Fourth tergite quite black, with a silvery crossband at an anterior margin. Tas. ....
       ....*C. rieki*, sp. nov., ♂
21.   Seven to 8 pairs of frontal bristles. Larger species, *c.* 8 mm in length. N.S.W., S.A., W.A. ....*C. flavifrons* Macquart, ♀
       Nine to 10 pairs of frontal bristles. Smaller species, 6-6.5 mm in length. A.C.T., Qld., W.A. ....*C. unguiculata*, sp. nov., ♀
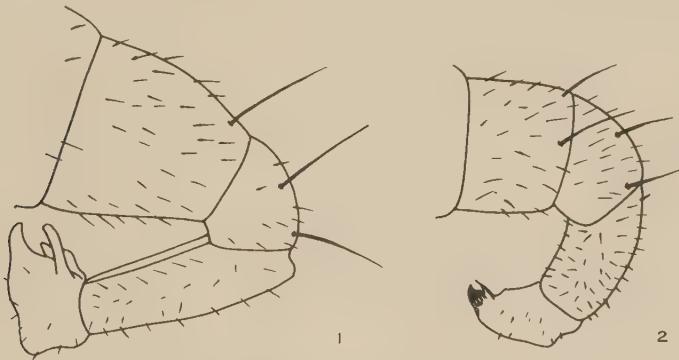
Fig. 1.—*Cylindromyia sydneyensis* Malloch: ♀ genitalia.
Fig. 2.—*C. atratula* Malloch: ♀ genitalia.

CYLINDROMYIA ATERRIMA, sp. nov., ♂

Whole body, including wings and halteres carbon-black; head and thorax with silvery spots, abdomen with a weak silvery shine.

Head with silvery shine, varying with angle of incidence of light; only frontal stripe dark brown, nearly black. Occiput in profile very developed, especially on lower three-fourths, convex, covered with short

yellowish hairs, cerebrale (middle area of occiput) bare. One pair of very strong verticals directed backwards. Ocellar triangle slightly sunken, ocellar bristles directed forwards; parafrontalia with very short and not numerous black hairs; about 12 frontal bristles, rather weak and decussate. Cheeks in profile very narrow, narrower than 3rd antennal joint, bare. Face in profile slightly keeled, protruding in relation to the cheeks, bare, straight, not elevated except slightly at mouth. Two strong vibrissae present, and some very weak vibrissal hairs. Jowls low, occupying about one-quarter of vertical diameter of eyes. Antennae long, nearly reaching the mouth, 3rd joint very long, broadening towards the apex, and there rounded. Arista 3-jointed, long, thin, bare. Vertex occupying about one-quarter of head width. Head distinctly broader than thorax and thorax broader than abdomen, the latter strongly compressed from the sides.

Mesonotum shining, with silvery reflections on humeral calli and on notopleural areas; also with traces of silvery longitudinal striping. Chaetotaxy of thorax as in *C. fenestrata*. Wings very black. Bend of m_1 not rounded, angular, with a short veinlet directed downwards, situated rather far from hind margin of wing. Petiole of r_5 longer than r-m; r-m on the middle of the discal cell. The very characteristic long bristles at base of wing, etc. in *C. fenestrata* are quite absent.

Pulvilli short, tube-like, of equal size on all legs. Claws also comparatively short, shorter than last joint of tarsus, quite equal on all legs.

Abdomen very compressed from the sides, especially high in the 4th segment, the underside of this and the 3rd segment forming a keel. First segment, usually almost confused with the 2nd in other species, is here very well separated and without bristles. Second tergite with 3 strong bristles on each side, and with 2 median at hind margin; 3rd and 4th with 1 lateral bristle and 2 median at lateral margin, 5th with similar disposition of bristles but the median pair situated distinctly in front of hind margin, more discally.

Length of body 11.5 mm, of wing 2.5 mm.

Type (1 ♂, 16.ix.1950, Scottsville, Qld. (E. F. Riek)) in the Division of Entomology Museum, C.S.I.R.O., Canberra.

CYLINDROMYIA TRISTIS (Bigot), comb. nov.

Ocyptera tristis Bigot, 1878, Ann. Soc. Ent. Fr. (5)8: 45.

Bigot writes:

"♂. Long 14 mill. Abdomine, supernè macrochaetis binis ad apicem segmentorum. Antennis fuscis; frons, supernè, vittaque frontali, nigris; facie albido flavo; thorace cinereo nigro, vittis quatuor nigris, externis latis; scutello nigro; calyptris pallide cinereis et nigro marginatis; abdomine nigro, segmentorum basi, latè, cinero albido; alis cinereis, nervis latè fusco limbatis; pedibus nigris.

En dessus, une paire de macrochètes situés aux bords postérièurs des segments abdominaux. Antennes, bande frontale, haut du front, noirs; face blanchâtre, deux

lignes obliques, noires, au-dessus des antennes; thorax noir, à reflets gris, avec quatre bandes d'un noir luisant, les externes fort distantes, larges; écusson noir; cuillerons d'un gris blanchâtre, bordés de noir; abdomen d'un noir assez luisant, avec de larges reflets d'un blanc grisâtre à la base des segments; ailes grises, toutes les nervures largement bordées de noirâtre, base un peu fauve; pieds noirs. Australia."

This species is unknown to the author. Its large size (14 mm), dark margins to the lower calyptrae, and the presence of dark clouding along the wing veins separate this species from the others. It is possibly very close to *C. fenestrata*.

CYLINDROMYIA FENESTRATA, sp. nov., ♂

A large species closely related to *C. tristis* and *C. aterrima*. Easily distinguishable from *C. tristis* by (1) the presence on each side of the 2nd tergite of a large, transparent, yellowish spot occupying the greater part of the side of the tergite; (2) its reddish yellow antennae; (3) the absence of striping on mesonotum; (4) the nearly complete absence of silvery greyish dust on the abdomen, and other characters.

Face in profile straight, without tubercle beneath antennae, slightly elevated only at mouth. Antennae reddish, with very long 3rd joint (twice as long as the 2nd), but not reaching the epistoma. Face, parafacialia, and lower part of parafrontalia with a weak silvery shine. Frontal stripe and most part of parafrontalia dark. Third antennal joint at level of arista, as broad as at apex (in *C. aterrima* it is distinctly narrower than at apex).

Mesonotum and scutellum without greyish dust, there is a sort of striping, but it is very little developed; there are some longitudinal black stripes and some slightly browner. Sides of thorax with 3 vertical silvery stripes, better developed on coxae of all 3 pairs of legs. Legs black, pulvilli yellow. Outside of fore femora slightly whitish. Claws equally developed on all legs, distinctly longer than the last joint of tarsus, but shorter than last 2 joints together. Hind trochanter nearly bare. Halteres yellow. Squamae alares nearly milky white, with darker rim.

Abdomen distinctly clavate, narrow at base, widened and rounded in its apical part; the basal part laterally compressed. Shape of abdomen (as of whole body) very similar to the figure of *Vespocyptera petiolata* (Baranoff, Diptera, vii, 1934, pl. i). First tergite very short, with only one weak bristle at sides, the 2nd with 2-3 at sides, 2 median marginal and 1 at sides on hind margin, the 3rd with same disposition of bristles as in the 2nd; the 4th also, but the hind margin at sides with 2 or more bristles, the 5th with a complete row of bristles at hind margin.

Wings dark (not as intensely so as in *C. aterrima*), lighter towards the hind margin. First posterior cell closed, with a petiole as long as the vein *r-m*, this vein situated exactly on the middle of discal cell. The bend of vein m_1 extremely close to hind margin of wing, the distance slightly greater than the vein *r-m*. Vein closing discal cell strongly S-shaped. Base

of r_{4+5} with similar black, short bristles, underside of this vein with very long bristles; base of costa on underside also with some very long bristles.

Chaetotaxy: 2 long bristles on humeral callus; 2 closely situated notopleural bristles; 2 sternopleurals; 4-5 hypopleurals; pteropleurae without bristles; 5 strong mesopleurals; acrostichals practically absent; 4 pairs of presutural, and 3-4 pairs of postsutural dorsocentrals; 2 strong bristles on postalar callus; 1 presutural bristle; 1 (weak) sublateral bristle; 1 intra-alar bristle; 3 supra-alar bristles, the anterior one immediately behind the sutura very strong; scutellum with 3 pairs of strong bristles: apical pair of strongly crossed bristles, subapical very strongly diverging (the strongest), and one sub-basal.

Length of body 14 mm, of wing 10.5 mm.

Type (1 ♂, Gayndah, Qld. (Masters)) in Australian Museum, Sydney; cotype (1 ♂, same locality) in the Division of Entomology Museum, C.S.I.R.O., Canberra.

CYLINDROMYIA NIGRICOSTA Malloch

Cylindromyia nigricosta Malloch, 1930, Proc. Linn. Soc. N.S.W. **55**: 312, fig. 36.

To Malloch's description the author can add a description of the female: This species seems to be very variable in regard to two characters. The form of last portion of vein m_1 may be straight (as in fig. 36 of Malloch), slightly concave, or with a sharp concavity. The posteroventral region of the 2nd tergite usually bears a yellow transparent spot on each side; these spots may be nearly absent or very well developed on about half the ventral surface of the segment.

Very similar to the male, but with frons slightly broader and with 4 pairs of orbitals, claws and pulvilli comparatively short, shorter than the last joint of tarsi, of same size on all legs. Ovipositor very long, with 2 strong, nearly parallel, acute, curved spines. Hairs on abdomen distinctly shorter, about half length of bristles. Abdomen laterally compressed and keeled ventrally.

Specimens seen.—1 ♂, 10.i.1948, Tubrabucca, Upper Hunter district, N.S.W., 4300 ft, Barrington Tops (A. Musgrave and Aust. Mus. party); 2 ♀♀, 24.iii.1954, Guyra, N.S.W. (E. F. Riek); 1 ♀, Jan. 1925, Barrington Tops, N.S.W. (Sydney Univ. Zool. Exp.); 1 ♀, 24.vii.1951, Orange, N.S.W. (Miss Z. Liepa); 1 ♀, 29.iii.1951, 1♀, 21.iii.1951, Lee's Springs, A.C.T. (about 3500 ft) (S. J. Paramonov).

The flies run very quickly on the smooth bark of eucalypts, are usually very high, and are only captured with difficulty.

Type in the School of Public Health and Tropical Medicine, Sydney.

CYLINDROMYIA HOWEANA, sp. nov., ♂, ♀

From the *C. tristis* group, very closely related to *C. fenestrata*. Easily distinguishable from the latter by (1) smaller size, (2) less-developed yellowish spot at sides of 1st abdominal segment, (3) absence of rather

strong bristle laterally at the base of 1st abdominal segment, (4) black antennae, and (5) shorter hairs on the 1st and 2nd tergites, the longest of them on the sides of 1st tergite being about half as long as the bristles nearby (in *C. fenestrata* they are about one-fourth as long as the bristles).

Length of body 12.5 mm, of wing 9 mm.

Specimens seen.—2 ♂ ♂, 29.xi.1955 (one bearing type label), 1 ♀, 1.xii.1955, Lord Howe Island (S. J. Paramonov and Z. Liepa), on leaves of shrubs; not very common.

Sexual dimorphism is great: (1) last portion of m_1 is slightly concave or nearly straight in male, in female strongly concave; (2) the bend of it is broadly rounded in male, in female attenuated and with a short appendix; (3) claws in male very long, much longer than last joint of tarsi, in female short, about as long as the last joint of tarsi; (4) last tergite in male with 6-8 bristles, in female without bristles; (5) 3rd tergite with 6-8 bristles in male, with only 4 bristles in female. Type in the Division of Entomology Museum, C.S.I.R.O., Canberra.

CYLINDROMYIA BRUNNEA Malloch, ♂

Cylindromyia brunnea Malloch, 1930, Proc. Linn. Soc. N.S.W. 55: 315, fig. 40.

The author has seen only the type and can add these notes: (1) vein *r-m* distinctly beyond the middle of discal cell; (2) petiole of 1st posterior cel as long as *r-m*, clearly not in a straight line with the vein r_5; (3) along the costa there is a yellow colour but it is much less intense than that of *C. nigricosta*; (4) humeral and postalar calli reddish yellow; (5) there are lateral bristles on the 2nd and 3rd tergites, not only at hind margin, but also in the middle of lateral margin; (6) the abovementioned tergites always have a greyish pollinosity which in *C. flavifrons*, for example, is quite absent.

Type in the Division of Entomology Museum, C.S.I.R.O., Canberra.

CYLINDROMYIA TRICOLOR Malloch, ♀

Cylindromyia tricolor Malloch, 1930, Proc. Linn. Soc. N.S.W. 55: 315.

The author has seen one additional ♀ (25.xii.1934, Kurrajong Heights, N.S.W. (D. F. Waterhouse)). Crossvein *r-m* slightly before the middle of discal cell. Whole of thorax and legs deep black. Sides of 2nd and 3rd tergites with bristles only at hind margin.

Type in the School of Public Health and Tropical Medicine, Sydney.

CYLINDROMYIA ANGUSTISSIMIFRONS, sp. nov., ♂

Closely related to *C. flavifrons* but much smaller and distinguishable from all other species by its extremely narrow frontal stripe, which is about one-half as broad as ocellar triangle or about one-ninth as wide as frons.

Frons and face with dense silvery dusting, parafrontalia more with a golden tinge. About 8 pairs of frontal bristles. Ocellar triangle with 2 pairs of erect, diverging bristles. Jowls in profile extremely narrow, as broad as proboscis; cheeks only slightly broader, face in profile protruding over the cheeks, slightly concave. Antennae not reaching the mouth edge, brown, apex of 2nd and the base of 3rd joint yellowish; arista thickened in its basal third.

Thorax with dense white pollinosity, and 4 black short longitudinal stripes on the presutural area, the median pair of stripes very narrow. Sides of thorax with 3 silvery vertical stripes extending on to all 3 coxae.

Squamae alares, including edges, pure white. Venation and colour of wing similar to those of *C. flavifrons*. Legs black. Claws long, nearly straight; outer claws of fore legs with a distal round plate. Claws much shorter than in *C. flavifrons*, only slightly longer than last joint of tarsus.

Hind margin of last sternite with 2 strong lateral bristles and a row of 8 short spines (in *C. flavifrons* 6 lateral bristles and 2 median, isolated short spines).

Abdomen predominantly reddish, but with base and apex black. In appearance very similar to *C. flavifrons*, but about half as large.

Length of body 7 mm, of wing 5 mm.

Specimens seen.—4 ♂ ♂, 16.i.1952, 1 ♂, 23.i.1952, Mt. Gingera, A.C.T. 5500 ft, (K. R. Norris).

Type (♂, 16.i.1952, Mt. Gingera, A.C.T. (K. R. Norris)), and paratypes in the Division of Entomology Museum, C.S.I.R.O., Canberra.

CYLINDROMYIA RUFIFEMUR, sp. nov., ♂, ♀

Closely related to *C. flavifrons*, but easily distinguishable by its reddish femora.

Male

Head with silvery dust, frontal stripe brownish; about 11 parafrontal bristles. Face in profile nearly straight, elevated only at mouth edge, on equal level with cheeks. Cheeks in profile as broad as jowls. Antennae long, narrow, reaching the mouth edge, nearly parallel-sided, slightly attenuated at apex; arista as long as the very long 3rd joint of antennae.

Mesonotum black, without striping or markings, and with a poorly developed whitish dust, even humeral calli are only slightly dusted. The sides of thorax also with a sparse whitish pollinosity. Legs, including fore coxae, reddish. Tarsi dark, with very long claws on all legs. Squamae alares milky. Wings yellowish on their anterior half, venation as in *C. flavifrons*. Halteres reddish yellow.

Abdomen predominantly reddish, only base and apex black. Hind margin of last sternite only with 1 lateral bristle, no short spines or bristles in the median area.

Female

Very similar to the male, with usual differences of sexual characters, presence of orbital bristles, short claws, and other characters.

Length of body 9.5 mm, of wing 6 mm.

Distribution.—NEW SOUTH WALES: 1 ♂ (type), 31.x.1949, Salisbury Downs–Clifton Downs (S. J. Paramonov). QUEENSLAND: 1 ♂, 1 ♀, 19.xi.1947, Rannes (K. R. Norris (paratype); 1 ♀, 7.iv.1954, Surfer's Paradise (K. R. Norris); 1 ♀, 12.ix.1950, 30 miles W. of Collinsville (E. F. Riek).

Type in the Division of Entomology Museum, C.S.I.R.O., Canberra.

CYLINDROMYIA WESTRALICA, sp. nov., ♂

Belongs to the group with reddish legs.

Head with face and jowls reddish but covered with very dense silvery pollinosity. Face in profile distinctly concave. Cheeks in profile very narrow, as broad as 2nd antennal joint. Frons with dark brown frontal stripe. Vertex occupying about one-fifth of head width. Two basal joints of antennae reddish, 3rd joint brown, antennae short, by no means reaching the epistoma. Vibrissae very long, strong, decussate.

Thorax black, but humeral calli and the sides partly reddish. Mesonotum with a strong whitish pollinosity at sides on presutural area and along the anterior margin, with 4 black longitudinal stripes, remainder of mesonotum and scutellum shining black. Bristles on mesonotum extremely long, longer than the largest diameter of squamae alares. Halteres yellow. Squamae alares white, with yellow rim. Wings yellowish, the pigment diffused on the anterior part of wing. Bend of 4th longitudinal vein distinctly obtuse. Vein *r-m* on the middle of discal cell.

Abdomen reddish, partly darker, but not black; with some silvery fasciae on tergites and sternites. Bristles, as on whole body, extremely long and robust.

Length of body 7.5 mm, of wing 5.5 mm.

Type (1 ♂, King George Sound, W.A.) in the Australian Museum, Sydney.

CYLINDROMYIA ATRATULA Malloch

Cylindromyia atratula Malloch, 1930, Proc. Linn. Soc. N.S.W. 55: 314, figs. 38, 39.

The author can add nothing to Malloch's description.

Type in the School of Public Health and Tropical Medicine, Sydney.

CYLINDROMYIA SYDNEYENSIS Malloch

Cylindromyia sydneyensis Malloch, 1930, Proc. Linn. Soc. N.S.W. 55: 314, fig. 37.

The author can add nothing to Malloch's description.

Type in the Division of Entomology Museum, C.S.I.R.O., Canberra.

CYLINDROMYIA BICOLOR (Bigot), comb. nov., ♀

Glossidionophora bicolor Bigot, 1885, Bull. Soc. Ent. Fr. **1885**: 55.

This species is probably invalid. Bigot writes:

"♀. Long. 6 mill. Antennis, haustello, vitta frontali et facie nigris, facie et fronte utrinque cinereis; thorace nigro opaco, obscure cinereo vittato; scutello nigro; calyptris albis; (halteribus?); abdomine rufo, subtus, apice, longe recurvo, basi, apice late maculisque tribus dorsalibus, oblongis, nigris; pedibus nigris; alis pallidissime cinereis, basi parum testaceo tinctis. Australia. 1 specim. (ex mus. nostro)."

"*Glossidionophora.*—Generis Ocypterae similis, differt: haustello tenui, exserto, rigido, basi cubitato, capite aequilongo; antennarum segmento 3° ovali, parum secundo longiore, et, apice parum externe acuminato, cheto omnino nudo."

This species is unknown to the author and its systematic position is not clear. Bigot described it as the type species of a new genus *Glossidiono-phora*. The form of the 3rd antennal joint is not sufficient to establish a new genus, but possibly there are other characters of difference which justify establishing a new genus. If it should prove that this species belongs to the genus *Cylindromyia*, it would have to be renamed, as there are already two species named *Cylindromyia bicolor*, one by Wiedemann (Zool. Mag., iii, 37.54, East India), and the other by Olivier (1811, Encycl. Méthod, viii, 423, from Europe).

CYLINDROMYIA HOBARTANA, sp. nov., ♂

Closely related to *C. flavifrons*, but easily distinguishable by the obtuse angle of m_1, the nearly straight distal portion of this vein, the normal structure of all claws, the silvery dust on head and mesonotum, and the predominantly reddish abdomen (2 last segments also reddish).

Head silvery dusted. Frontal stripe wider than parafrontalia. About 11 pairs of frontal bristles. Antennae brownish. Proportions of the head as in *C. flavifrons*.

Humeral calli and notopleural area with strong silvery pollinosity. The middle black portion with 3 narrow, silvery, longitudinal stripes of equal width, extending only to the sutura. Sides of thorax predominantly silvery pollinose. Legs black, with silvery pollinosity of outer side of femora. All claws nearly of equal size, normal, long. No extremely long and dense hairs on internal side of hind femora. Halteres yellow. Squamae alares milky, with yellow rim. Wings not quite hyaline, darker along the costa.

Abdomen reddish, with black shining markings in the middle. Sides of 3rd and 4th tergites with silvery dust, having a triangular form on each side; also with dark spots at sides of tergites. Bristles extremely long; on 2nd, 3rd, and 4th, longer than segment itself. Hind margin of last sternite with 2 bristles on each side and 3-4 spines in the middle.

Length of body 9 mm, of wing 7.5 mm.

Type (1 ♂, 3.i.1953, Hobart, Tas. (E. F. Riek)) in the Division of Entomology Museum, C.S.I.R.O., Canberra.

CYLINDROMYIA DAYI, sp. nov., ♂

Closely related to *C. flavifrons*, with similar golden shine on head, but easily distinguishable by: (1) obtuse angle of vein m_1; (2) absence of very large and dense hairs on inner side of hind femora; (3) absence of very long and dense tuft of hairs on the hind coxae; (4) presence of a row of short spines at hind margin of last sternite. Squamae alare uniformly yellow, but it seems to be an unnatural colour, induced by an unknown factor.

Majority of characters as in *C. flavifrons*.

Length of body 10 mm, of wing 7 mm.

Specimens seen.—1 ♂ (type), 27.xi.1936, Killara, N.S.W. (M. F. Day).

The author names this species in honour of Dr. M. F. Day, to whom he is indebted for some very interesting insects, collected mostly at Killara.

Type in the Division of Entomology Museum, C.S.I.R.O., Canberra.

CYLINDROMYIA FLAVIFRONS (Macquart)

Ocyptera flavifrons Macquart, 1851, Dipt. Exot. suppl. iv. pt. 2. p. 214.

Cylindromyia flavifrons, Malloch, 1929, Proc. Linn. Soc. N.S.W. 54: 291.

This species is one of the most common in Australia. The male can easily be differentiated from those of other species by the following characters: (1) hind trochanters with a tuft of very long, curly hairs; these are distinctly longer than the diameter of hind femora, and directed downwards; long hairs also present on underside of hind femora; (2) all claws equal, very long, about as long as 2 last joints of tarsi combined; (3) outer side of fore femora with silvery dust; (4) face in profile with a distinct tubercle immediately beneath base of antennae, in general distinctly concave; (5) last section of vein m_1 distinctly S-shaped and with a small veinlet at bend; (6) last sternite with 2 short, closely situated, curved spines at middle of hind margin; (7) frons and face normally golden.

The female usually differs from the male in having: (1) silvery dust on frons and face; (2) very short claws on all legs, the claws only as long as the last joint of tarsi; (3) hind trochanters without tufts of hairs.

Distribution.—NEW SOUTH WALES: 1 ♂, 22.x.1949, Nyngan–Bourke (S. J. Paramonov); 1 ♂, 12.iii.1920, Creel, Mt. Kosciusko; 1 ♂, 2.xi.1923, Manly; 1 ♂, 2.ii.1916, Roseville; 1 ♂, 12.ix.1923, Gunnedah (L. Hiskisson); 1 ♂, 24.xi.1949, Wilcannia–Mt. Boppy (S. J. Paramonov); 2 ♂♂, 1.xii.1950, Lake George (K. R. Norris); 1 ♂, 2.i.1936, Kurrajong Heights (D. F. Waterhouse); 1 ♂, 1 ♀, Jan. 1928, Barrington Tops (Benham); 1 ♂, 1 ♀, 19.xi.1949, Fowler's Gap (S. J. Paramonov); 1 ♀, 18.x.1923, Manly; 1 ♀, 24.xii.1930, 1 ♀, 3.i.1931, Yass (K. English); 1 ♀, Sydney (W. W. Froggatt Coll.). AUSTRALIAN CAPITAL TERRITORIES: 1 ♀, Feb. 1929, Canberra (G. F. Hill); 1 ♀, 28.ii.1949, 1 ♀, 20.ii.1950, 1 ♀, 11.xii.1951, Canberra (S. J. Paramonov); 1 ♀, 31.xi.1951, Canberra (K. R. Norris); 1 ♂, 1 ♀, 27.iv.1946, Canberra (E. F. Riek); 1 ♀, 25.xi.1949; 1 ♂, 4.i.1935, Blundell's (W. Rafferty); 1 ♂, 1 ♀, 15.iii.1950, Blundell's (S. J. Paramonov); 2 ♂♂, 25.xi.1947, Cotter R. (S. J.

Paramonov); 3 ♂♂, 7.xi.1947, Paddy's R. (S. J. Paramonov); 1 ♂, Nov. 1934, Orroral, near Canberra (M. Fuller). SOUTH AUSTRALIA: 1 ♂, 21.x.1951, National Park (E. F. Riek); 1 ♀, 20.i.1921, Adelaide (A. Tonnoir); 1 ♀, 9.xi.1946, Adelaide (H. M. Cane). WESTERN AUSTRALIA: 1 ♂, 1.xi.1938, Wagin (K. R. Norris); 1 ♂, 19.ix.1933, 2 ♀♀, 23.x.1933, Cranmore Park, Perth (M. Fuller); 1 ♂, 24.x.1936, 1 ♀, 4.xi.1936, Guildford (K. R. Norris); 1 ♂, 23.xi.1938, 1 ♂, 25.xi.1938, Coolup (K. R. Norris); 1 ♂, 24.ix.1934, Rottnest I. (K. R. Norris); 4 ♂♂, 14.x.1934, Cannington (K. R. Norris); 1 ♂, 20.x.1933, Fremantle (K. R. Norris); 1 ♂, 14.ix.1934, Carnac I. (K. R. Norris); 1 ♂, 3.ix.1914, Geraldton (J. Clark); 1 ♀, 15.xi.1924, Perth (Nicholson); 1 ♀, 11.x.1934, Beverley St. Farm, Perth–Albury Rlwy. (M. Mackerras). 1 ♀, no data.

The author has examined the abovementioned specimens.

CYLINDROMYIA RIEKI, sp. nov., ♂

Closely related to *C. flavifrons,* but distinctly smaller, the pollinosity of head not golden but silvery, all claws broadening at apex in form of a small black disc; the rest of the claw is yellow (in *C. flavifrons* the claws are of usual form, i.e. apically acute). The black marking on the 3rd tergite broad, connecting with a similar marking of the 2nd tergite, and becoming confluent at hind margin with a black crossband.

Middle part of mesonotum with only 1 narrow silvery longitudinal stripe (as in *C. flavifrons*).

Length of body 8 mm; of wing 5 mm.

Type (1 ♂, 20.i.1949, Eagle Hawk Neck, Tas. (E. F. Riek)), in the Division of Entomology Museum, C.S.I.R.O., Canberra.

CYLINDROMYIA UNGUICULATA, sp. nov., ♂, ♀

Closely related to *C. flavifrons,* but much smaller, with silvery pollinosity on the head and thorax, with deformed fore tarsal claws in male, without long and dense hairs on inner side of hind femora in male, and other characters.

Head black, with silvery pollinosity on face and frons, frontal stripe black, slightly broader than parafrontalia. Ten pairs of frontal bristles. Frons in profile distinctly concave. Antennae deep black, comparatively short, by no means reaching the epistoma.

Mesonotum with silvery pollinosity at sides, and 1 narrow, median, longitudinal, presutural stripe. Legs black, coxae covered with silvery pollinosity; on outside of fore femora with similar but less conspicuous pollinosity. Male with claws on fore legs distinctly longer than on mid and hind legs, the outer claw deformed, bearing an apical, transparent, black-rimmed disc. Hind coxae and inner side of the hind femora in male with usual hairs, these not so unusually long and dense as in *C. flavifrons.* Squamae alares pure white. Halteres black.

Wings greyish on whole surface. Vein m_1 at bend forms a right angle, the last portion of this vein is nearly straight (in *C. flavifrons* it is S-shaped).

Abdomen with black colour more developed than in *C. flavifrons*, but in this character the species is rather variable and the author is not quite sure that two species are not hidden under a single name. He has, however, examined about 30 specimens from more or less adjacent localities and it seems unlikely that two new, closely-related species would be distributed together in the same area. The hind margin of last sternite bears, as in *C. flavifrons*, only 2 short spines.

Female similar to male, with only the usual sexual differences: short claws, orbital bristles, broader vertex.

Length of body 6-6.5 mm, of wing 4 mm.

Distribution.—AUSTRALIAN CAPITAL TERRITORIES: 1 ♂, 1 ♀ (type), 4.xi.1953, Blundell's (S. J. Paramonov); 5 ♂ ♂, 1 ♀, 27.x.1953, 11 ♂ ♂, 1 ♀ (paratype), 28.x.1953, Canberra (S. J. Paramonov); 1 ♂, 5.xi.1934, Black Mountain, Canberra (W. Rafferty); 1 ♂, 3.xi.1948, 5 ♂ ♂, 7.xi.1947, 1 ♂, 19.xi.1947, Paddy's R. (S. J. Paramonov); 1 ♂, 1.xi.1947, Cotter R. (S. J. Paramonov). QUEENSLAND: 1 ♂, 18.xi.–3.xii.1930, Meteor Downs, near Springsure (I. M. Mackerras). WESTERN AUSTRALIA: 2 ♀ ♀, 14.x.1934, Cannington (K. R. Norris).

The last two specimens are doubtful.

Type in the Division of Entomology Museum, C.S.I.R.O., Canberra.

CYLINDROMYIA (PLESIOCYPTERA) PACIFICA Bezzi

Cylindromyia (Plesiocyptera) pacifica Bezzi, 1928, Diptera of the Fiji Islands, p. 199.

CYLINDROMYIA BIMACULA (Walker), comb. nov.

Ocyptera bimacula Walker, 1849, List. Dipt. 4: 694.

Walker writes:

"Nigra, capite flavo, abdomine rufo, basi apice maculisque duabus nigris, antennis pedibusque nigris, alis subcinereis.

Body black, clothed with black hairs and bristles; head yellow, clothed beneath with hoary hairs; a black stripe between the eyelets and the feelers; sides of the face fringed with bristles at the base; epistoma hardly prominent; eyes pitchy, not hairy; palpi black; feelers black, as long as the face; third joint club-shaped, much longer than the second; bristle much longer than the third joint, stout near the base, very slender from thence to the tip; chest adorned in front with three hoary stripes; scutcheon and abdomen armed with a few black spines; abdomen red, longer than the chest; base and tip black; two black spots on the back, one of them connected with the black of the base; legs black, clothed with black hairs and bristles; foot-cushions pitchy; wings slightly gray; wingribs pitchy; veins black, pitchy at the base; tip cross-vein forming an almost right angle with the fourth longitudinal vein, joining the third longitudinal vein at some distance before the tip of the latter; lower cross-vein nearly straight; scales white, with yellow borders. Length of the body 4½ lines, of the wings 6 lines.

Van Dieman's Land. Presented by the Rev. T. Ewing."

Dr. Fritz van Emden kindly informed the author:

"Of *Ocyptera bimacula* the British Museum has the type and a paratype. Both are well preserved and I can find no trace of palpi."

It is quite evident that Walker has made a mistake, and this species belongs probably to the genus *Cylindromyia*. Not having the material from Tasmania it is impossible to decide what species was described by Walker. The colour of legs and abdomen, as well as the venation, are rather good characters for recognition of this species.

OCYPTERA? DIVERSA Walker

Ocyptera? diversa Walker, 1856, Insecta Saundersiana, London, 1: 262.

The generic position of this species was doubted by Walker himself. He writes:

"Nigra; caput auratum, antice album, subtus canum; abdomen basi testaceum; pedes rufi, femoribus anticis basi tarsisque nigris; alae sublimpidae, ad costam fuscae.

This species does not belong to any of the genera into which the Ocypteratae have been divided.

Black, shining: head pale gold-colour, hoary beneath; frontalia deep black, broad, almost linear; face white; its facialia without bristles; epistoma slightly prominent; facialia of the peristoma beset with bristles; mouth pitchy; eyes with small facets; feelers black; third joint compressed, obliquely rounded at the tip, nearly twice the length of the second joint; abdomen full twice the length of the chest; first segment cylindrical, with a large testaceous spot on each side of the hind border; second and following segments together spindle-shaped, broader than the first, and about twice its length; second testaceous along the fore border; tip curved beneath; legs red; fore-thighs black towards the base; feet black; wings almost colourless, dark brown along the fore border for full one-third of the breadth; first posterior areolet closed on the border of the wing; prae-brachial vein almost straight beyond its flexure; veins black; alulae whitish with pale yellow borders; halteres yellow. Length of the body 5 lines; of the wings 8 lines.

Van Diemen's Land."

Dr. Fritz van Emden kindly informed the author:

"There is no trace in the British Museum of *Ocyptera diversa* Walk. or of any other *diversa* Walk. under Tachinidae except a *Cryptopalpus*, a very different stout and large fly from S. America. In my own work here I have never found types of Walker's described in Insecta Saundersiana, and enquiries in Oxford were in each case also negative."

Genus SARALBA Walker

Saralba Walker, 1864, Proc. Linn. Soc. Lond. 8: 114.

Type species *S. ocypteroides* Walker, loc. cit.

Walker writes:

"Mas. Corpus angustum, subcylindricum. Caput thorace paulo latius. Oculi nudi. Proboscis acuta. Palpi graciles, subclavati. Antennae breves, subgraciles; articulus 3us fusiformis, 2° duplo longior. Abdomen basi subcompressum, thorace fere duplo longius. Pedes robusti. Alae angustae.

Allied to *Ocyptera*. Male. Body narrow, nearly cylindrical. Head a little broader than the thorax; frontalia linear; epistoma slightly prominent. Eyes bare. Proboscis acute. Palpi slender, subclavate. Antennae rather slender, about half the length of the face; third joint fusiform, twice the length of the second; arista slender, more than twice the length of the third joint. Abdomen with many short bristles, slightly

compressed towards the base, nearly twice the length of the thorax. Legs stout, setose. Wings narrow; praebrachial vein forming a curve at its flexure, joining the cubital vein at the tip of the wing; discal transverse vein slightly undulating, parted by less than half its length from the border, and by much less than its length from the flexure of the praebrachial vein."

Townsend (1938, Manual of Myiology, vii, 26) adds the following diagnosis:

"Length, 10 mm. Elongate and narrow; black, thorax gold fasciate, abdomen pale yellow basally. Head little wider than thorax, clypeus flush, epistoma fully 1/3 as long as wide and gently warped, oral margin axis nearly as long as antennal, palpi slender subclavate and bowed, antennal axis 2/3 head height and well above eye middle, third antennal joint little over twice second, arista not twice as long as third antennal joint, male vertex 1/5 head width and equibroad frontalia 6 times parafrontal width, parafacialia equibroad and 1/2 width of facialia, cheeks 1/5 eye length. Two PS (postsutural dorsocentrals) and St (sternopleural bristles). Male wings narrow, 5R (fifth radial, first posterior or apical cell) neck petiolate in wing tip, R5 (fifth radial or third longitudinal vein) bristled at base, M1 (first medial vein) slightly arcuate inward, M3 (third medial vein) its length from cubitulus, latter rounded. Male abdomen subcylindric, subcompressed basally and much widened from hind 1/2 of second segment posteriorly, 1/2 longer than thorax, MM (median marginals) of abdominal segments on second but weak on first segment, MR (marginal row of bristles) on third and fourth segments, ventral membrane narrowly exposed. Male fifth sternite neither cleft nor emarginate.

Known only from New Guinea."

Saralba ocypteroides Walker

Saralba ocypteroides Walker, 1864, Proc. Linn. Soc. Lond. 8: 114.

Walker writes:

"Mas. Nigra, capite pectoreque argenteis, frontalibus atris linearibus antice aurato marginatis, palpis testaceis, thorace fasciis duabus cinereis subauratis, abdomine nigricanti-cinereo spatio basali et segmentorum marginibus pallide cinereis vitta dorsali nigra interrupta, femoribus posterioribus basi flavescentibus, alis cinereis dimidio basali nigricante.

Male. Black. Head silvery white; frontalia deep black, linear, with gilded borders in front where the eyes diverge from them; facialia without bristles. Palpi pale testaceous. Thorax with two cinerous slightly gilded bands; second band abbreviated; sides slightly bristly. Pectus silvery. Abdomen semihyaline, blackish cinereous; borders of the segments and the whole of the basal part pale cinereous; a black dorsal line, interrupted on the fore border of each segment. Posterior femora yellowish towards the base, this hue most extended on the hind femora. Wings cinereous, blackish on half the breadth from the costa; veins and halteres black; alulae lurid, with blackish borders. Length of the body 4½ lines; of the wings 8 lines."

Saralba bancrofti, sp. nov., ♂

As *S. ocypteroides* is very poorly studied, the comparison of the new species with it is not easy.

Head broad, but distinctly higher than broad; ground colour of head yellowish. Frontal stripe very dark brown, nearly black, parafrontalia with golden shine, face and whole head below the antennae with white

pollinosity, but dull. Frontal stripe quite parallel-sided, in region of the vertex the parafrontalia tend to narrow almost to extinction. Frontal stripe with 2 rows of erect, dense (but not contiguous), moderately strong bristles, orbitals absent; 2 moderately strong ocellar bristles, directed forward; verticals very poorly developed; 2 postverticals are stronger than verticals. Vertex occupying about one-fifth of head width. Occiput with whitish pollinosity, with short, but rather numerous white hairs and the usual row of black short bristles on the upper half. Cheeks extremely narrow in profile, about as broad as a half width of the 2nd antennal joint. Jowls also narrow, occupying about one-seventh of head height, with very short and rather sparse light hairs; bristles at sides of the mouth cavity absent. Vibrissae short and weak; besides these there are only 5-6 pairs of short black bristles on the face, the face and cheeks being quite bare. Antennae brownish, their apices reaching to about mid-point of face. Arista rather long, bare, 3-jointed, the 2 basal joints very short. Proboscis short, fleshy; palpi yellowish, very thin.

Mesonotum with pattern very similar to that of *Zosteromyia* B. & B.; with 2 golden crossbands, 1 band from one notopleural area to another, a second one in front of scutellum; the remainder velvety black.

Humeral calli with 2 bristles; postalar calli with 2 bristles; only a pair of acrostichals in front of scutellum; 2 pairs of dorsocentrals (one weak) in presutural area, and 3 pairs (two weak) in postsutural area; 2 pairs (one weak) of supra-alar bristles; 1 pair of intra-alar bristles in region of postalar calli; 1 pair of presutural bristles. On the sides of thorax: 2 strong sternopleurals, 4 hypopleurals, 5 mesopleurals, 1 pteropleural; golden fascia from notopleural area extending to sternopleurae, the latter silvery. Scutellum black, but apical area lighter, 4 bristles; apical crossed, sub-basal nearly parallel.

Halteres yellow. Lower squama alaris yellow, upper one whitish. Legs black, pulvilli long and yellowish. Hind and mid femora yellow, only the apical quarters black; fore femora with yellow spot on underside at base. Hind tibiae thickened, especially in the apical half.

Wings yellowish, slightly more intense along the costa. First posterior cell closed, with a very short petiole. Discal cell very long, vein r-m on the middle of discal cell. The band of m_1 is rounded, very close to the hind margin of wing.

Postscutellum and metanotum with a yellow pollinosity.

Abdomen $1\frac{1}{2}$ times longer but narrower than thorax, slightly broadening towards the apex; basal half of abdomen round in section but apical half distinctly depressed from above. Bristles weak, a little stronger only on hind margin of 3rd tergite. Last sternite at hind margin with strong, numerous, but short bristles. The last tergite forming a round, acute edge at hind margin. First segment and the basal half of the 2nd yellowish, transparent; tergites with a narrow brownish median stripe, remainder of

abdomen irregularly brown. The last tergite with a distinct greyish pollinosity.

Length of body 9.5 mm, of wing 8 mm.

Type (1 ♂, Eidsvold, Qld. (T. L. Bancroft)) in the Division of Entomology Museum, C.S.I.R.O., Canberra.

THE TABANIDAE (DIPTERA) OF AUSTRALIA

I. GENERAL REVIEW

By I. M. Mackerras*

Contents

Summary

About 230 species of Tabanidae are now known to occur in Australia, Tasmania, and the Torres Strait islands. Nearly 90 per cent. belong to four ancient tribes, which are widely distributed and successful in the southern hemisphere, namely: Pangoniini (18 Australian species), Scionini (63), Bouvieromyiini (38), and Diachlorini (92). The more recent Oriental element comprises 20 Tabanini and one *Chrysops*. A small, retrograde, Papuan migration is included in the figures for Bouvieromyiini and Diachlorini.

About 190 specific names are accepted as valid, there are more than 120 synonyms, 28 described species remain unrecognized, and about 40 species are undescribed.

Many of the species can be identified at present only by reference to the Ferguson Collection in the School of Public Health and Tropical Medicine, University of Sydney, and the information about them is scattered in many papers. The primary purpose of this series, therefore, is to arrange the species in accordance with modern classification, present keys and adequate descriptions to facilitate their identification, and record what is known of their biology.

In the present Part, an attempt is made to provide the basic historical and practical information that will assist the new student of the family, together with a key to the subfamilies and tribes, and the references for the whole series. The tribes will be reviewed individually in subsequent Parts of this series.

I. Introduction

During a period of about 15 years, interrupted by service in Palestine, and ending with his untimely death in 1927, Eustace Ferguson had set about amassing a representative collection of Australian Tabanidae.

* Queensland Institute of Medical Research, Brisbane.

He sent specimens to the British Museum for comparison with types preserved there, had a long correspondence with E. E. Austen and G. A. K. Marshall about them, examined some of Macquart's types in the Paris Museum, corresponded with other authorities abroad, and, in short, took particular pains to authenticate the names he attached to his specimens. As a result, the Ferguson Collection, which is now in the School of Public Health and Tropical Medicine, University of Sydney, has been an indispensable tool for workers on the family ever since.

Ferguson died before he could integrate his studies, and it has consequently been difficult for anyone in the past 30 years to do effective work on the family, unless he had access to the collection. The need has long been felt for a comprehensive revision, which would enable workers in the field to recognize their species, and thus serve as a foundation for future research.

I have attempted to provide such a revision in this series of papers. It will be limited to species that occur within the territorial boundary of Australia, including Tasmania, the coastal islands, and the Torres Strait islands, and is planned to appear in the following sequence:

    I. General review.
    II. Subfamily Pangoniinae, tribe Pangoniini.
    III. Subfamily Pangoniinae, tribe Scionini.
    IV. Subfamily Chrysopinae.
    V. Subfamily Tabaninae, tribe Tabanini.
    VI. Subfamily Tabaninae, tribe Diachlorini.

It seemed desirable to check all of Ferguson's determinations, so far as it has been possible to do so. Types preserved in Australia have been traced, and specimens compared with them. Specimens of every Australian species known to me have been submitted to Mr. H. Oldroyd, of the British Museum (Natural History) for his opinion, usually on specific questions of identity. Comparatively few remain identified from descriptions alone, and there are grounds for accepting Ferguson's identifications of nearly all of these.

The generic names used for Pangoniinae and Chrysopinae in this Part may be taken as reasonably established, except that it may prove necessary to resurrect *Copidapha* End. for the Australian species at present included in the subgenus *Pseudoscione*. The review of genera and subgenera of Tabaninae is, however, not yet complete, and consequently the names now employed for them are provisional. No change seems likely in *Tabanus,* as restricted to species with setulae on the basicosta; but *Cydistomyia* is used quite broadly for generalized Diachlorini with bare eyes in the female, and *Dasybasis* for those with obviously hairy eyes. Modern generic names, rather than those of the original authors, have been used for clarity in the historical section of the paper.

One specific name has been changed. The species referred to in previous papers (Mackerras 1955*a*, 1955*b*) as *Mesomyia* (*Lilaea*) *abra* (Philip, 1941) should be known as *fuliginosa* (Taylor, 1916), which is an earlier synonym of *notata* (Ricardo, 1915), preoccupied.

The collections on which the work has been based are enumerated in Section VII.

II. History

The development of our knowledge of the Australian Tabanidae may be conveniently divided into three sections: descriptive and taxonomic; life-histories; parasites and relation to infection.

(a) *Descriptive and Taxonomic*

Description of species and their arrangement in a system of classification have followed much the same pattern in most groups of Australian insects. Broadly, there is the nineteenth-century period, in which insects were sent by collectors to workers in England and Europe, who described them (often very inadequately) and retained the types in their own institutions; the first 40 years of the twentieth century, in which Australian workers played an increasingly active part in describing and revising their species; and the post-war period, in which the "modern taxonomy" is displacing the old. The last has scarcely touched the Tabanidae, partly for the reason given in the Introduction, but mainly because, in the present state of our knowledge, it is impossible to breed and handle them experimentally. This is a limitation which applies to the vast majority of animals, and we must learn to attain the same ends, although perhaps less convincingly, by observational methods.

The first Australian Tabanidae to be named were two of our best known species of *Scaptia* (*auriflua* and *guttata*) by Donovan in 1805. He was followed by Latrielle in 1812 with one species, an echo of Baudin's exploration of Kangaroo I., and by W. S. Macleay in 1826 with two. Macleay's contribution is of special interest, as it was the first on the family by a worker in Australia. He described two northern species, *roei*, which has remained unrecognized, but may be the same as *Scaptia conspicua* (Ric.), and *cinerescens*, which is a striking species of *Tabanus* in the Northern Territory. Mr. J. R. Henry has searched the Macleay Collections for me, but failed to find a type of either species.

Descriptive work went on actively during the next 74 years. Altogether, 130 species were described during the century, of which 60 are recognized as valid today. They are distributed among the following modern genera: *Austroplex* 2, *Ectenopsis* 2, *Caenoprosopon* 1, *Scaptia* 27, *Mesomyia* 2, *Tabanus* 7, *Cydistomyia* 6, and *Dasybasis* 13. This considerable accretion of knowledge is summarized in Table 1.

Australian material influenced the classification of the family very little, most of the species being absorbed into the old genera *Tabanus* and

Pangonius, which was soon corrupted to *Pangonia,* and later split by Rondani (1863) into the subgenera *Diatomineura, Erephopsis,* and *Corizoneura.* All these names are familiar in Australian synonymy, but another old genus, *Silvius,* appeared only twice, although it became more prominent after 1901. Three monotypic genera had Australian genotypes, *Ectenopsis* Macquart, 1838, and *Dasybasis* Macquart, 1847, which are still valid, and *Apocampta* Schiner, 1868, which has fallen as a synonym of *Scaptia.* Walker's (1850) subgenera of *Pangonia* were ignored for many years, but one, *Clanis* (a homonym), was monotypic

TABLE 1

AUSTRALIAN SPECIES OF TABANIDAE NAMED IN THE PERIOD 1805-1899

Author	Years	Valid	Synonyms or Homonyms	Unrecognized
Donovan	1805	2	—	—
Latreille	1812	1	—	—
Macleay	1826	1	—	1
Wiedemann	1828	3	1	—
Guérin	1831	1	—	—
Macquart	1834	1	—	1
Westwood	1835	1	—	—
Macquart	1838	5	2	2
Erichson	1842	3	—	—
Macquart	1846-55	14	14	9
Walker	1848-57	23	13	10
Newman	1857	1	—	—
Jaennicke	1867	—	2	—
van der Wulp	1868	—	1	—
Thomson	1868	—	1	—
Schiner	1868	1	1	1
Bigot	1892	3	9	1
Bergroth	1894	—	—	1

for an Australian species, and Australian genotypes were selected for three others by Coquillett in 1910. These were *Scaptia, Plinthina,* and *Lilaea,* which are recognized today as valid at the generic or subgeneric level.

Descriptive work abroad continued during the first quarter of the twentieth century, particularly at the British Museum, where Miss Ricardo began in 1900 to bring order into existing knowledge by publishing annotated regional catalogues. After working on other regions for several years, she returned to the Australian fauna in an important series of papers published between 1914 and 1917. Altogether she established 47 valid specific names, the largest number by any single worker on Australian Tabanidae.

In Australia, there was a remarkable gap of 85 years from 1826 to 1911, during which nothing was published. The silence was broken by Froggatt (1911) with a catalogue, brief descriptive notes, and good illustrations of some common species, and he was quickly followed by Taylor (1913), who was the first entomologist of the newly established Australian Institute of Tropical Medicine at Townsville. Interest in the family was stimulated by the work at the Institute, by a suggestion that Tabanidae might transmit bovine onchocerciasis, and by rapidly growing collections, largely built up by enthusiastic amateur entomologists, among whom T. L. Bancroft, G. A. Waterhouse, H. J. Carter, A. Jefferis Turner, and G. M. Goldfinch were especially prominent. The result was a vigorous flow of publications, which are summarized in Table 2.

TABLE 2

AUSTRALIAN SPECIES OF TABANIDAE NAMED IN THE PERIOD 1900-1955

Author	Years	Valid	Synonyms or Homonyms	Unrecognized
England and Europe				
Ricardo	1900	1	1	—
Austen	1912	1	—	—
Summers	1912	2	4	—
Surcouf	1912	—	—	1
Ricardo	1913	1*	1*	—
Austen	1914	—	1	—
Ricardo	1914-17	45	8	—
Enderlein	1925	—	4	1
Philip	1941	—	1	—
Australia				
Taylor	1913	3	3	—
White	1915	3	—	—
Hardy	1916	—	1	—
Taylor	1916-20	31	41	—
Ferguson and Henry	1920	8	2	—
Ferguson and Hill	1920-22	16	4	—
Ferguson	1921-24	15	5	—
Hardy	1939-48	1	2	—
English	1949-55	2	—	—
Mackerras	1955	3	—	—

* Described from New Guinea.

This table does not give a complete picture of the work that was done. Ferguson and his associates gave at least as much attention to unravelling the rapidly growing synonymy as to describing new forms, and Ferguson, in his 1924 and 1926 papers on the genus *Scaptia*, was preparing the foundations for a wider revision of the whole family. Hardy also attempted to clarify synonymy and to reduce the old composite genus *Tabanus* to some sort of order. However, he relied largely on original descriptions,

so his results lack the precision that Ferguson and Hill achieved. The types of the new species described in Australia have remained in Australia, except those of Arthur White (1915), which are in the British Museum.

Valid Australian genera or subgenera established during the period were:

Pangoniinae—*Caenoprosopon* Ricardo, 1915; *Palimmecomyia* Taylor, 1917; *Parasilvius* Ferguson, 1921; *Austroplex* Mackerras, 1955; *Leptonopsis* Mackerras, 1955; *Therevopangonia* Mackerras, 1955; and *Myioscaptia* Mackerras, 1955.

Chrysopinae—*Pseudotabanus* Ricardo, 1915; *Pseudopangonia* Ricardo, 1915; *Phibalomyia* Taylor, 1920; and *Vepriella* Mackerras, 1955.

Tabaninae—*Cydistomyia* Taylor, 1919; and *Paracanthocera* Enderlein, 1923.

TABLE 3

SUMMARY OF AUSTRALIAN SPECIES OF TABANIDAE NAMED IN THE PERIOD 1805-1955

Period	Valid	Synonyms	Unrecognized	Total
1805-1899	60	44	26	130
1900-1955	132	78	2	212
Totals	192	122	28	342

So far as species are concerned, the whole of the foregoing may be summarized in Table 3. The figures in this table are approximate. Some of the recognized species are of doubtful validity, and some of the unrecognized species are probably not Australian. In addition, there are about 40 new species to be described in this series of papers, bringing the total known in Australia to about 230, a substantial fauna, the relationships of which will be examined in a later section.

(b) Life-histories

The habitats and behaviour of the adults vary greatly in the different groups, and information about them can scarcely be said to have a history, as it consists, in most instances, of little more than brief notes at the end of formal descriptions. All the Australian workers were energetic collectors, and it is surprising that, except for Hill, they wrote so little about what the insects did. Our knowledge of life-histories is also meagre, but it is important, and it is therefore convenient to review it here.

There is published information about the early stages of only 14 Australian species. This is a reflection, not so much of lack of interest, as of the difficulty that workers have experienced in finding the larvae and pupae. Moreover, no one has yet succeeded in inducing any of our

species to lay viable eggs in captivity, although Hill was able to rear adults of *Tabanus townsvilli* Ric. from egg masses collected in the field. The records are summarized chronologically in the following list:

Taylor (1917)
>   *Mesomyia* (*Pseudotabanus*) *australis* (Ric.)   Egg

Johnston and Bancroft (1920*b*)
>   *Tabanus particaecus* Hardy   Larva, pupa
>   *Tabanus townsvilli* Ric.   Larva, pupa
>   *Mesomyia* (*Lilaea*) *fuliginosa* (Tayl.)   Pupa

Hill (1921)
>   *Tabanus pallipennis* Macq.   Egg, larva, pupa
>   *Tabanus townsvilli* Ric.   Egg, larva, pupa
>   *Tabanus nigritarsis* Tayl.   Larva, pupa
>   *Mesomyia* (*Lilaea*) *fuliginosa* (Tayl.)   Larva, pupa

Fuller (1936)
>   *Scaptia* (*Scaptia*) *auriflua* (Don.)   Larva, pupa

Fuller (1937)
>   *Dasybasis froggatti* (Ric.)   Larva, pupa
>   *Dasybasis gentilis* (Erichs.)   Larva, pupa
>   *Dasybasis neobasalis* (Tayl.)   Larva, pupa

English (1949)
>   *Dasybasis oraria* (Eng.)   Larva, pupa

English (1953)
>   *Ectenopsis* (*Ectenopsis*) *angusta* (Macq.)   Larva, pupa

English (1955)
>   *Scaptia* (*Pseudoscione*) *vicina* (Tayl.)   Larva, pupa
>   *Scaptia* (*Myioscaptia*) *muscula* Eng.   Larva, pupa

In addition, Miss English has the larva and pupa of *Dasybasis indefinita* (Tayl.) still unpublished, and Mr. Alan Dyce has reared a remarkable, new metallic *Cydistomyia* from rot-holes in *Casuarina* trees.

The important feature of the list is that it contains the only known larvae and pupae of Pangoniini, Bouvieromyiini, and generalized Diachlorini, and the only ones known in Scionini other than the Nearctic *Goniops chrysocoma* (O.-S.).

(c) *Parasites and Relation to Infection*

Transmission of disease by blood-sucking insects was prominently in the minds of workers in the first quarter of the present century, particularly in the tropics. All groups came under suspicion, and any parasites found in them were regarded as of special interest. Tabanidae had been incriminated in the transmission of surra and loiasis, and had been

accused of spreading anthrax. Their rôle in spreading tularaemia was not demonstrated until much later.

This trend naturally influenced Australian workers, and nearly all the parasites recorded belong to this period. They were:

Protozoa.—*Leptomonas* sp. Seen in smears of the intestine of *Tabanus strangmani* Ric. and *Dasybasis circumdata* (Walk.) at Eidsvold, Qld., by Johnston and Bancroft (1920*a*).

Helminths.—Larval filarioid worms, which they named *Agamofilaria tabanicola,* were found by Johnston and Bancroft (1920*a*) in *D. circumdata* at Eidsvold, and subsequently by Henry (1927) in *D. circumdata* and *D. innotata* (Ferg. & Hen.) at Kendall, N.S.W. Stages of development were described, from small larvae in the abdominal fat to long, slender ones at the base of the proboscis. The vertebrate host of this parasite is still not known.

Mermethid worms have been recorded by Hill (1921) from a larva of *Tabanus pallipennis* at Townsville, Qld., and by English (1949) from a pupa of *Dasybasis oraria* in south coastal New South Wales.

Hymenoptera.—Chalcid parasites were recorded from the proboscis of adult Tabanidae by Nicholls (1920), and from the hindgut of "several species" by Henry (1927).

Acarina.—Erythraeid mites of the genus *Leptus* have been seen on adult Tabanidae, but neither the mites nor their hosts have yet been identified (R. Domrow, personal communication).

Onchocerciasis ("worm-nodule") of cattle is the only important infection which Tabanidae have been suspected to transmit in Australia. Numerous observations were made by searching captured Tabanidae for developing larvae; by inducing captured flies to feed on the cut surface of worm nodules, and subsequently dissecting them; by feeding captured flies on clean calves, either individually in tubes or free in an insectary; by observing flies feeding naturally on clean calves, and subsequently examining the calves for development of nodules; and, in one instance, by inoculating heads of flies containing larval filarioid worms into the skin of an apparently clean bullock. The following list shows the species of Tabanidae investigated by one or more of these methods:

McEachran and Hill (1915). Northern Territory.—*Mesomyia* (*Lilaea*) *mansoni* (Summers), *Tabanus pallipennis*, *T. strangmani*, *T. cinerescens* Macl., *T. nigritarsis*, and two unidentified species.

Cleland, Dodd, and Ferguson (1916). Milson Island, N.S.W.—Two unidentified species (apparently *Dasybasis circumdata* and possibly *D. regis-georgii* (Macq.)).

Dickinson and Hill (1917). Northern Territory.—*Tabanus strangmani* and *T. nigritarsis.*

Johnston and Bancroft (1920*a*). Eidsvold, Qld.—*Tabanus strangmani, T. australicus* Tayl., *Dasybasis circumdata, D. dubiosa* (Ric.).

Rheuban and McGown (in Cilento 1923). Townsville, Qld.— *Tabanus townsvilli* and *Cydistomyia germanica* (Ric.).

Henry (1927). Kendall, N.S.W.—An extensive series of investigations carried out from 1917 to 1920; 12,684 females of 33 species dissected; 19 species given opportunity to feed on clean calves in a fly-proof pen; five species fed on juice containing *Onchocerca* larvae from cut surface of nodules.

TABLE 4

DISTRIBUTION OF THE TRIBES OF TABANIDAE

Subfamily and Tribe	Holarctic	Neotropical	Ethiopian	Oriental	Austro-Malaya and Pacific	Australia	New Zealand
PANGONIINAE							
Pangoniini	++	+++				18	1
Scionini	+	++++			12	63	6
Philolichini			++++	+	→ 3		
SCEPSIDINAE		+	+				
CHRYSOPINAE							
Bouvieromyiini	+	+	+++	+	← 6	38	
Chrysopini	++++	+++	+++	++	→ 3	1	
Rhinomyzini			+++	+			
TABANINAE							
Diachlorini	+	++++	++	+	78*	92	9
Haematopotini	+++		++++	+++			
Tabanini	++++	+++	++++	++++ →	60*	20	

* Approximate estimate only.

Except for suggestive, but uncontrolled, observations recorded by Cilento, and the discovery of developing filarioid larvae, which, however, Johnston and Bancroft considered on morphological grounds not likely to be *Onchocerca,* all the results obtained were negative. There was reason to doubt that Tabanidae were concerned in transmitting bovine onchocerciasis even before *Culicoides* was shown to be the vector in Malaya.

Following American work, Mackerras, Mackerras, and Mulhearn (1942) examined the possibility that *Anaplasma marginale* might be spread among cattle mechanically by the bites of Tabanidae. They used interrupted feeds by *Dasybasis circumdata,* transferring the flies quickly from the infected to the clean animal. The results were negative, and the findings from parallel experiments with *Stomoxys calcitrans* (L.) and with needles indicated that this method of transmission was unlikely to influence the epidemiology of the infection appreciably in Australia.

III. Composition of the Australian Fauna

Of the 10 tribes (counting the Scepsidinae as a tribe) into which the Tabanidae are divided, six occur on the mainland of Australia, and another is represented in the Austro-Malayan division of the region. Their distribution is shown in Table 4, abundance in other regions being indicated by plus signs, and occurrence in the Australasian region by the numbers of species at present known. For the purpose of the table, Austro-Malaya and Pacific includes the festoon of islands from Celebes to Samoa, and Australia includes the mainland, the Torres Strait islands, and Tasmania. Arrows indicate the probable direction of migration across the boundary between the Oriental and Australasian regions.
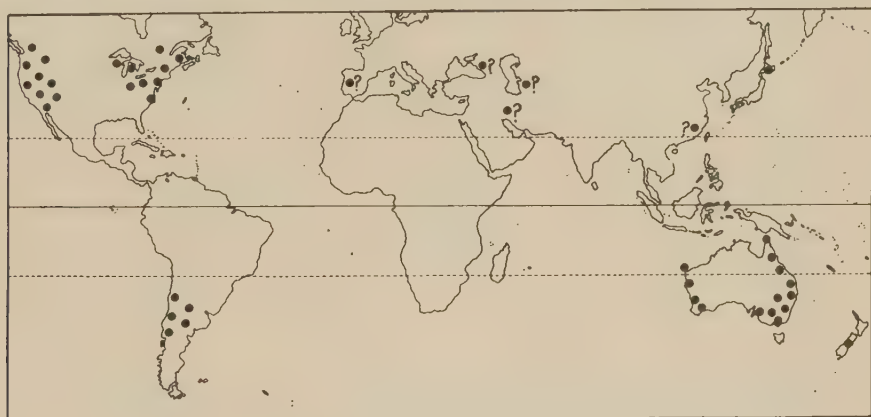
Fig. 1.—Distribution of generalized Pangoniini (Group 1).

The striking feature of the Australian fauna is that it contains the largest assemblage of generalized Pangoniini, Scionini, Bouvieromyiini, and Diachlorini in the world, about 205 species, or 88 per cent. of our whole tabanid fauna. They dominate the more recent Chrysopini and Tabanini over most of the country, as the marsupials dominate the eutherian mammals, and they present basically similar zoogeographical problems, although with important variations, which become apparent when the tribes are examined separately.

PANGONIINI

The Australian genera belong to the more primitive section of the tribe (Mackerras 1955a) which has the following distribution (Fig. 1): Australia 18 species, New Zealand 1, South America 8, North America 20, Palaearctic possibly 8. This kind of distribution is often used as an argument for the northern origin of older groups of animals. It would seem, however, to be more in accord with the geological history of America to suggest that it is the result of a northern migration along the Andean corridor by southern groups which are adapted to live in a temperate climate.

The tribe has a peripheral distribution in Australia, but has not been found in Tasmania nor the islands of Bass Strait. It seems likely that Tabanidae disappeared from Tasmania during the Pleistocene, except for a small endemic group of *Dasybasis,* the bulk of the present fauna being derived from a post-Pleistocene invasion of *Scaptia* and *Dasybasis* from the mainland. The climate is probably still too cold and wet to favour Pangoniini and Bouvieromyiini, although the latter have reached Flinders I.

SCIONINI

Here, too, the Australian species belong to an unspecialized part of the tribe, the genus *Scaptia,* which is divided into six subgenera, three being known only from Australia, one from Australia, New Guinea, New Zealand, and South America, one from Australia and South America, and one from South America only. I had previously (1954) included Africa
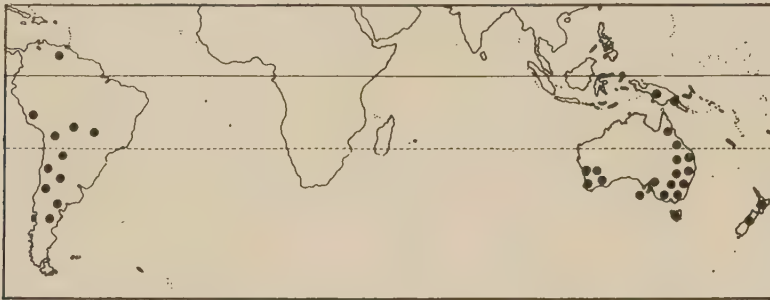
Fig. 2.—Distribution of the genus *Scaptia* (Scionini).

in the distribution; but Oldroyd (personal communication) has shown the records to be unreliable, and specimens of two of the supposedly South African species, which he sent me, proved to be the Australian *S. testaceomaculata* (Macq.) and *S. ruficornis* (Macq.). Figure 2 shows the corrected distribution of the genus.

Local distribution will be discussed in Part III of this series. Briefly, the evidence indicates that there has been a major centre of recent evolution in south-eastern Australia, with radiation south, north, and west, and development of secondary centres of evolution in north Queensland and south-western Western Australia. Radiation from these has led to some retrograde invasion of the original eastern centre by the subgenus *Plinthina* from the west and the *concolor* group of *Pseudoscione* from the north.

BOUVIEROMYIINI and DIACHLORINI

The tribes just discussed differ in their distribution in the northern hemisphere, in the extent to which they have invaded the southern tropics, and in their success (as judged by numbers of species and abundance of individuals) in the southern countries; but they have one important

feature in common: no species of either is known from the Ethiopian or Oriental regions. They are, in fact, typical representatives of the "Antarctic" or "southern Gondwanaland" element in the Australian fauna.

I believe that the Bouvieromyiini and Diachlorini evolved and dispersed together, so it is convenient to consider them under one head. They differ from one another, in that the Diachlorini have been much the more successful and widely ranging of the two, although the absence of Bouvieromyiini from New Zealand may have been due to extinction during the Pleistocene glaciation, as suggested by Paramonov (1955) for some other groups of Diptera. They differ from Pangoniini and Scionini, in that both occur in southern and eastern Africa, the Malagasy subregion, and sparsely in the Oriental region, as well as in South America and Australia (Figs. 3 and 4).
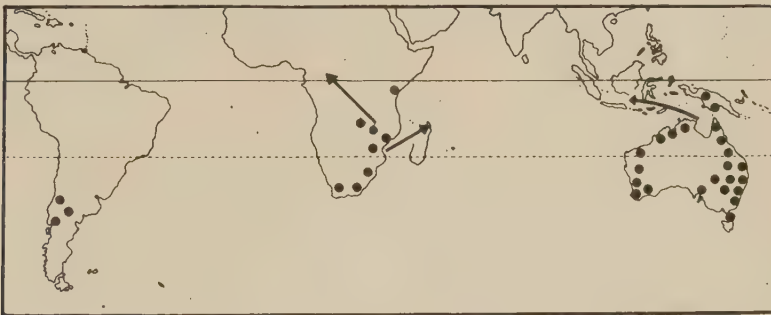
Fig. 3.—Distribution of the genus *Mesomyia* (Bouvieromyiini). Arrows indicate outlying distribution of related genera.

The special problem presented by these two tribes may be stated quite simply. There is clear evidence of affinity between their southern, hairy-eyed forms in South America, southern Africa, Australia, and (in Diachlorini) New Zealand. By reason of their distribution, both in the hemisphere and locally in Australia, they must be included in the southern Gondwanaland element in this country. On the other hand, their northern forms distinctly suggest a Lemurian distribution around the Indian Ocean. This suggestion is stronger in Diachlorini (Fig. 4) than in Bouvieromyiini (Fig. 3), and is further strengthened by the fact that the Oriental gap is just as wide in *Philoliche*, which undoubtedly entered the Austro-Malayan division of the region from the west (Mackerras 1954, Fig. 6).

It would be easy to suppose that there are two elements, a southern Gondwanaland and a Lemurian, in each tribe, for both are well established in other groups of animals. The difficulty is that the smooth, northern forms are at least as closely related to the hairy, southern ones as they are to those on the Lemurian arc. One should be able to distinguish the elements more clearly, if they were really distinct. Moreover, similar resemblances can be seen also in tropical South American Diachlorini.

My present view is that both tribes should be included in the southern Gondwanaland element, that there has been parallel evolution in the warmer parts of the three regions, and that the Lemurian arc of distribution represents a "pincer movement", one prong extending north-west from Africa approaching another extending north-east from Australia.

Further light may be thrown on this problem by a study of the Austro-Malayan and Pacific species, which is now being undertaken.

Fig. 4.—Distribution of Diachlorini around the Indian Ocean.
● Unspecialized genera. ○ Specialized genera.

CHRYSOPINI and TABANINI

These tribes stand in striking contrast to those discussed above. Chrysopini are represented in north Queensland by a single species of *Chrysops*, which is the end-point of a chain leading back to the substantial development of the genus in the Oriental region. The species of *Tabanus* are more numerous. They are most abundant in the north, extend down the east coast into New South Wales, and disappear in the south, there being one record in Victoria, none in Tasmania or South Australia, and two rather uncommon species in south-western Western Australia. As with *Chrysops*, there is a continuous chain leading back to the Oriental fauna, with which almost all the Australian species show clear evidence of affinity.

To summarize, the Australian tabanid fauna is dominated by four ancient tribal elements, which are part of a much more widespread, primitive, but highly successful, southern fauna. To this must be added a moderate, more recent Oriental invasion, and a small, retrograde migration from New Guinea.* There is no definitely Lemurian element on the mainland, although the northern Bouvieromyiini and Diachlorini could possibly belong to one.

* *Mesomyia* (*Pseudotabanus*) *demeijerei* (Ric.), *Cydistomyia palmensis* (Ferg. & Hill), and *C. torresi* (Ferg. & Hill) in north Queensland and the Torres Strait islands.

This kind of faunal composition is common in Australia, the only unusual feature of the present example being the extent of the relationship with South Africa. It could be explained, including the otherwise puzzling suggestions of Lemurian as well as southern relationships, by the splitting of a once continuous Gondwanaland-Antarctic fauna, and subsequent contact with the more recently developed Chrysopini and Tabanini; but most geologists would not accept such an explanation. It does not seem to me that the biologist can contribute much more from studies of comparative morphology and recent distribution — we must wait for fresh evidence from other directions, before the different points of view can be reconciled.

The other divisions of the region may be reviewed briefly in order to complete the general picture.

The Austro-Malayan and Pacific Tabanidae may be taken together. They were derived from two sources: mainly from Australia, but substantially also from the Oriental region. The southern elements include the Scionini, Bouvieromyiini, Diachlorini, and a few *Tabanus*, about 100 of the 160 species in the area (Table 4). The western elements are *Philoliche, Chrysops,* and most of the *Tabanus*. New Guinea has been a vigorous centre of evolution. Apart from *Tabanus ceylonicus* Schin., which extends from the Oriental region to the Solomon Islands (and also into north Queensland), *Tabanus innotabilis* Walk., which ranges from northern Australia to the Solomons, and a few of more limited distribution, all the species in the area are endemic. Moreover, the larger groups have developed a recognizable "Papuan facies", and a few small, distinctive subgenera or genera (*Pareucompsa, Neobolbodimyia, Japenoides,* etc.) have evolved locally. The most successful genera are *Tabanus,* which reaches the outer limit of the family in Samoa (but misses New Caledonia), and the Australian *Cydistomyia,* with nearly 50 species in New Guinea, and "Papuan" tongues extending westward to Celebes, east to Fiji, south-east to New Caledonia, and south back to Australia.

The New Zealand Tabanidae show no indication of continuity with the Austro-Malayan fauna. Pangoniini are represented by a monotypic subgenus of the Australian genus *Ectenopsis;* Scionini by six species of *Scaptia (Pseudoscione),* which are more like their South American relatives than those in Australia and New Guinea; and Diachlorini by an endemic subgenus of *Dasybasis;* there are no Chrysopinae or Tabanini.

IV. COLLECTION AND PRESERVATION IN THE FIELD
(a) Adults

One cannot lay down fixed rules for collecting adults — the keen general collector often brings in more specimens than the person who is searching for Tabanidae only. An eye attuned to their appearance and movement and an ear to their note are, however, useful aids. If they are

numerous and interested in human blood, it pays to sit quietly and take them as they come; if they are scarce, it is often more profitable to move slowly through the bush, stopping immediately the note of one is heard. Species that fly round the head are easy to see, but some approach the boots or ankles very unobtrusively, even when their general flight is noisy. A quiet horse or cow is often a better bait than man, and some species are attracted to the tyres of a motor-car heated by travel on hot, sunny roads. It is good practice to move quietly round one's car and examine all the tyres, whenever one returns to it.

Species that do not suck blood (and some that do) may often be collected when they are seeking the nectar of flowers. *Leptospermum* blossoms are by far the most attractive in eastern Australia, especially in high country. A good grove of *Leptospermum* in somewhat swampy soil, freshly in flower, is a dipterist's paradise on calm, sunny days, anywhere over 3000 ft above sea level. The bushes are crowded with insects; species of *Scaptia, Dasybasis,* and occasionally some of the rarer genera vie with *Pelecorhynchus,* Nemestrinidae, and Bombyliidae; there is a leavening of Stratiomyiidae (*Odontomyia*), Asilidae, Therevidae, and the smaller muscoids; and the whole assemblage is dominated by the large, brilliant species of *Rutilia* and *Amenia* (Tachinidae). Males, particularly *Scaptia, Pelecorhynchus,* and *Trichophthalma,* may be seen hovering and gyrating over sunny open spaces, where they are extraordinarily difficult to capture. Species of other orders, especially Coleoptera and Hymenoptera, are equally numerous and active. Many of the records in Part III of this series will be from *Leptospermum* flowers.

Low myrtaceous shrubs of the sand plain in Western Australia are almost equally attractive (Calaby, personal communication), but other flowers are not often visited, although Taylor took *Paracanthocera australis* (Ric.) on *Eugenia,* an occasional species has been seen on *Melaleuca* and *Grevillea,* and a few on coastal heath. A few species, chiefly Pangoniini, have only been seen flying low over the ground, or resting on shrubs, bracken, or grass.

Light traps have been little used in this country; but the only males I have seen of *Tabanus innotabilis* and *Cydistomyia clavicallosa* (Ric.) were taken by Mr. A. K. O'Gower in a light trap at Townsville, and several northern species enter houses at night, so the method is worth a wider trial. The forest canopy has also been neglected. Recent work has shown it to be an important habitat of Tabanidae, as well as mosquitoes, in Africa (reviewed by Oldroyd 1954) and Panama (Fairchild 1953). Species collected on the tree-platforms included a significant proportion that were unknown or rare at ground level. Tropical America and Africa have much richer faunas of arboreal mammals than we have in Australia; nevertheless, trials of canopy platforms might prove interesting here, especially in rain-forest, where Tabanidae are usually rare on the ground.

Two novel methods of collecting deserve mention as they have brought in considerable numbers of males, which are notoriously difficult to obtain by conventional means. Bequaert (1932) listed 26 species of Tabanidae, including four that were new, and the males of 21, which Mr. Herbert Lang collected in the Belgian Congo by robbing wasps (*Bembex bequaerti* var. *dira* Arnold) as they brought the flies back to their burrows in the bank of a river. He had a colony of several thousand *Bembex* under observation, and found that, if he released a wasp after depriving it of its prey, it would soon return with another. Similarly, I have seen three interesting species of New Zealand Tabanidae, which the late H. Hamilton collected from nests of *Rhopalum* sp. (Crabronidae) at Ohakune in the North Island. The wasps evidently sample habitats which are inaccessible to human collectors.

The other method was reported by Philip (1952). He collected six species of Tabanidae, including the males of four, in recognizable condition from "pitchers" of the carnivorous plant, *Sarracenia flava* L., in Florida, U.S.A. Only one of the species was seen on the wing during the period. I have searched pitchers of *Nepenthes* for mosquito larvae, but have not so far seen any Tabanidae in them.

Whatever the method of collecting, a medium-sized entomological net is indispensable, because, even when using oneself or a companion as bait, shy species are difficult to tube, and will rarely give one a second chance. It is desirable to carry at least two (preferably three or four) 4×1 in. cyanide tubes, and I always kill and pin my specimens immediately in the field. Tabanidae are easily rubbed, and valuable characters destroyed, so they must never be crowded in a killing-bottle with other insects, and always handled gently when pinning them. It is not good practice to set Tabanidae (or any Diptera) other than to draw their legs into easily seen positions when they are fresh.

As valuable information can be obtained by comparing series from different localities, it is important always to collect as many specimens as time will permit. Labels should include, not only locality and date, but a note of the colour of the eyes (especially of bands) and of what the insect was doing when it was captured.

(b) Early Stages

Larvae and pupae are very difficult to find; indeed, one needs something of the genius for fossicking, which was so highly developed in the late Mary Fuller. That some of her most interesting discoveries were by-products of collecting bait for unorthodox trout fishing in no way detracts from their value.

As regards habitats, the larvae of *Tabanus* so far found have been aquatic, while prepupae of *Mesomyia* have been collected close to water, and their younger stages may be presumed to be aquatic also. Most of the

others have been terrestrial, usually living among grass-roots or under debris in somewhat damp soil; but *Dasybasis oraria* breeds in the sand of sea beaches, and the larvae of *Scaptia muscula* were found in association with ant-lion larvae in dry sand on the floor of horizontal clefts in sandstone (English 1955). The species of *Cydistomyia*, which breeds in rotholes in *Casuarina* trees, has already been mentioned.

Pupae may be kept in muslin-covered jars, partly buried in some of the soil or other material in which they were collected. Adults will usually emerge within a few days, and the shells are as useful for taxonomic purposes as whole pupae. It is convenient to impale the shell on the same pin as the insect that emerged from it.

Larvae are more difficult to deal with. Most are predacious, and it is necessary to separate them into individual jars or tubes, in which they can be fed on short segments of earthworms or soft-bodied insect larvae. Miss English keeps a culture of *Ephestia* for the purpose. Patience is needed, because it is often necessary to wait a year, or even two, before the larvae will pupate. Fortunately, they usually seem to do better if left undisturbed for considerable periods than if they are constantly being looked at.

It is desirable to preserve some larvae by dropping them into boiling water, and then transferring them to 80 per cent. alcohol (or Carnoy's fluid, if their histology is to be studied), but most should be kept for rearing. When they pupate, a careful search should be made for the cast larval skins, because they are useful for descriptive purposes as well as for correlation. They can be preserved in 80 per cent. alcohol.

V. MORPHOLOGY

This section is intended simply as a practical guide for the student who has not worked on the family previously. Most of the characters can be indicated clearly enough by means of labelled diagrams (Figs. 5-8), but some require discussion. As in earlier papers, a conservative terminology is used throughout, without prejudice to questions of homology or of priority in the use of anatomical names. Additional information will be found in Oldroyd's (1952, 1954) volumes on African Tabanidae.

(a) Colour

The colours of pinned specimens gradually fade and change over the years, even when they are kept in the dark. I have several times been temporarily deceived into thinking that fresh specimens did not belong to the same species as the old material with which I was comparing them. *Scaptia divisa* (Walk.), for example, is almost black when freshly caught, whereas old specimens are a dull brownish red. Old specimens may be freshened considerably, as well as greasy ones cleaned, by immersion overnight in amyl acetate (a method for which I am indebted to Dr. C. B.

Philip), but the colours are rarely completely restored. For this reason, and because even fresh material varies appreciably, I have used ordinary, simple colours and their combinations in the descriptions, rather than any more elaborate system based on colour charts.

As mentioned earlier, it is important to note colours and banding of the eyes when the specimens are freshly caught, because they nearly always become uniformly brown or blackish within a few days of death. Except in old or dirty specimens, enough of the colour for descriptive purposes may usually be restored by leaving the insect for a few hours in a relaxing box. I generally put them in the box in the morning, record colours and markings in the evening, and return those in which the colours have not developed to the box again until next morning. Too long an exposure or too wet an atmosphere is liable to make the whole specimen bedraggled and greasy looking, a condition from which it is difficult to restore it.

Bands are not always restored by relaxing, but may show up if the eye is painted with a drop of benzol or one of the proprietary wetting agents. As a final test, Oldroyd (1954) recommends Goffe's solution, which consists of:

Glacial acetic acid	1 part
Glycerine	1 part
Mercuric chloride (0.1 per cent. in water)	1 part
Alcohol (90 per cent.)	48 parts

The head is detached, and dropped face downwards into the fluid in a small, glass-stoppered jar, so that the eyes are immersed. The stopper is replaced, and the head left to soak. The colours may appear in 15-20 min, or it may be necessary to leave the head in the fluid overnight. The head may be subsequently dried and gummed to a strip of card attached to the pin carrying the specimen, but the tomentum is spoiled, and its appearance should be recorded before the eyes are treated.

(b) Head

The presence or absence of hairs on the eyes is often a more useful character than their colour or pattern, but it has the limitation that there is every gradation both in length and density of the hairs. I have arbitrarily accepted eyes as "hairy", when the hairs can be seen at ×15 by illuminating the surface of the eye obliquely or tangentially.

The upper anterior facets of the eye are often more or less enlarged in male Tabanidae, and they may be sharply marked off from the smaller, darker, lower and posterior facets. The appearance may be striking, for example, in many Chrysopini and Tabanini; but enlargement is so variable in degree and capricious in occurrence in other tribes, that it would seem at present to be of greater interest to the physiological ecologist than to the systematist.

The *ocellar tubercle* is clearly defined in Australian Pangoniinae and Chrysopinae, but it has to be distinguished from the *vertexal triangle** in the females of Tabaninae. This is an equilateral or isosceles triangle, with its base at the vertex and its apex pointing down the frons, which is often differentiated by being more raised, more hairy, darker, or more shiny than the rest of the frons. The ocellar tubercle, when developed, usually lies near or at its apex (Fig. 5*C*). In the males, the tubercle, when visible at the vertex (Fig. 5*D*), is more clearly homologous with the ocellar tubercle of the other subfamilies.

The *frons index* is defined here as:

$$\frac{\text{length of frons from vertex to junction with subcallus}}{\text{width of frons at its mid length}}.$$

Care is needed in comparing indices recorded by different authors, because the methods of measurement vary (see, for example, Hardy 1948, Oldroyd 1954). The frons is said to *diverge* when it widens towards the subcallus, to *converge* when it narrows.

The antennae are composed basically of a *scape, pedicel,* and 8-segmented *flagellum,* and these terms are frequently used by modern workers, instead of the old first, second, and 8-annulate third segments. The terminology fits most Pangoniinae very well; but the flagellum in other groups is compacted, the 4 basal segments being fused and more or less enlarged to form a *basal plate,* from which the apical 4 project as a clearly differentiated *style* (Fig. 5*F*). There is nothing flagellum-like about this structure, and the subdivisions are more like annuli than segments, even in Pangoniinae, so the old terms have convenience as well as usage to support them. It is unfortunate that the word "style" is used in two senses in the family. I have not been able to find a convenient alternative to either, so will qualify by referring to "antennal" or "of ♂ hypopygium" whenever there may be any possibility of confusion.

The palpi are 2-segmented in Tabanidae. However, only the 2nd, generally more conspicuous, segment is usually meant when the word is used without qualification.

The mouthparts of Tabanidae have been illustrated many times, and the female is always shown as having fully developed mandibles and maxillae. It was also observed that species of *Scaptia* which did not suck blood had mandibles as large as those that did, in contrast with *Pelecorhynchus,* in which the mandibles of the female were always considerably reduced (Mackerras and Fuller 1942). Oldroyd (1954 and personal communication) has shown that the females of *Tabanotelum* (Diachlorini), *Thaumastocera,* and *Sphecodemyia* (Rhinomyzini) have no mandibles. I have since found in Australian Pangoniini that mandibles are fully developed in the female of *Austroplex,* reduced in *Ectenopsis*

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* I prefer "vertexal", in spite of its incorrect formation, to "vertical", which has a different meaning in ordinary usage.

(s.s.) and *Parasilvius*, and absent in *Caenoprosopon** and *Therevopangonia*. Possession of a full complement of mouthparts in the female can no longer be regarded as a family character of the Tabanidae.
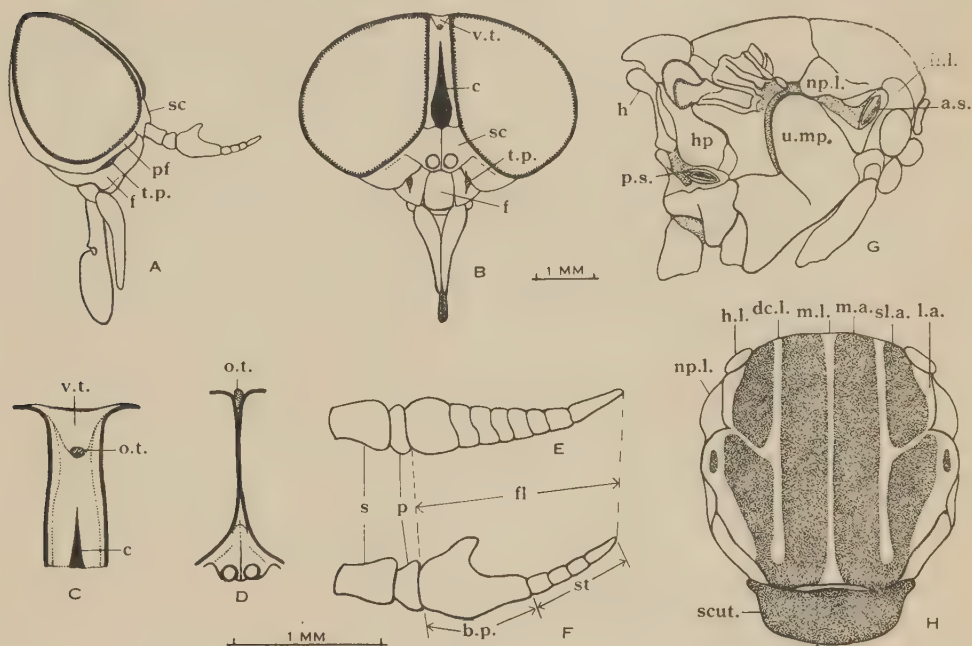
Fig. 5.—*A, B*, head of *Cydistomyia alternata* (Ferg. & Hill), ♀ : *v.t.*, vertexal triangle; *c*, callus; *sc*, subcallus; *pf*, parafacial; *t.p.*, tentorial pit; *f*, face. *C*, enlarged upper part of frons of same: *o.t.*, ocellar tubercle. *D*, frons of *Cydistomyia doddi* (Tayl.), ♂. *E*, antenna of *Scaptia* (*Pseudoscione*) *maculiventris* (Westw.), ♀, *F*, of *Cydistomyia alternata*, ♀ : *s*, scape; *p*, pedicel; *fl*, flagellum; *b.p.*, basal plate; *st*, style. *G*, side of thorax of *Cydistomyia pseudoardens* (Tayl.), ♀ : *h.l.*, humeral lobe; *np.l.*, notopleural lobe; *u.mp.*, upper mesopleural convexity; *hp*, hypopleural convexity; *a.s.*, *p.s.*, anterior and posterior spiracles; *h*, halter. *H*, dorsum of thorax of *Scaptia* (*Plinthina*) *vertebrata* (Big.), ♀ : *m.l.*, median line; *m.a.*, median area; *dc.l.*, dorso-central line; *sl.a.*, sublateral area; *l.a.*, lateral area; *scut.*, scutellum.

(c) Thorax

The scutal pattern is illustrated in Figure 5*H*. The basic form would appear to be a dark scutum, on which pale lines or vittae may develop in the median line, in the position of the dorsocentral bristles of Muscoidea (for which reason I prefer the term "dorsocentral" to "sublateral"), and along the transverse suture. The *median area* of

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* I was in error in an earlier paper (Mackerras 1955*b*, p. 621) in stating that the female of *Caenoprosopon* lacked maxillae. Further dissections have shown that the stylets observed were really the maxillae, which were separated from the palpi and displaced towards the base of the labrum-epipharynx in the specimens originally studied.

ground colour lies between the dorsocentral lines, and the *sublateral areas* lie outside them. The *lateral areas* are not separated from the sublateral by any clear anatomical boundary, but they are usually differently coloured, and it is convenient to recognize them. When the pale vittae are wide, the appearance changes completely, the basic ground colour becoming a series of wide, dark stripes (three or four, depending on whether the median pale line is developed) on a lighter ground. Some common patterns are illustrated in Plate 1.

The pleurae are uniform in configuration and distribution of hairs, and do not assist in defining genera or species, although the hairs are longer and denser in some than in others. The conspicuous tufts on the upper mesopleural and hypopleural convexities are occasionally useful. Oldroyd (1949) has noted that the thoracic spiracles of Diachlorini are usually widely open, whereas those of Tabanini are generally provided with large lips.

(d) Wing

I have continued to use Tillyard's (1926) modification of the Comstock-Needham system of notation (Fig. 6*A*), although some minor
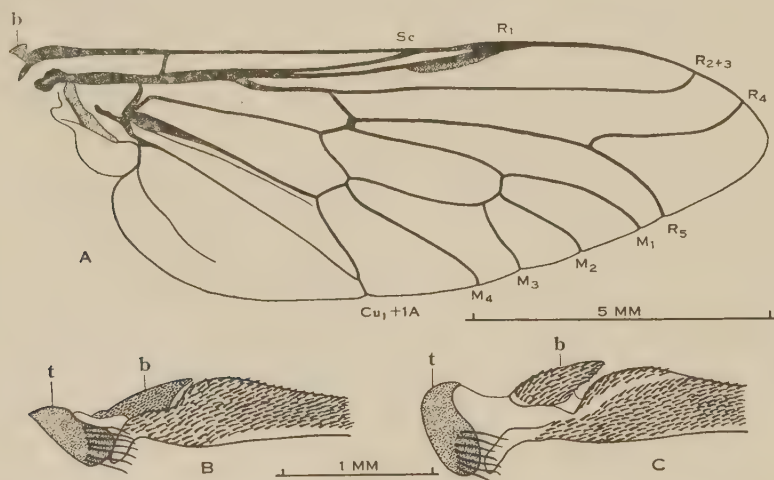
Fig. 6.—*A*, wing of *Scaptia* (*Scaptia*) *patula* (Walk.), ♀, showing notation. *B*, base of wing of *Cydistomyia alternata* (Ferg. & Hill), ♀, *C*, of *Tabanus nigritarsis* Tayl., ♀: *b*, basicosta; *t*, tegula.

changes might be indicated. Thus, Barretto (1946) considers the vein here labelled R_4 to be R_{3+4}; and I feel that M_4 may really be $M_4 + Cu_{1.1}$, the so-called *m-cu* crossvein being the basal part of $Cu_{1.4}$. Both are questions of interpretation, which do not seem capable of proof in the present state of our knowledge, and it does not seem justified to upset existing stability to incorporate them.

The "appendix" to R_4, shown only as a small knob in the figure, but often of considerable length, is in a different category, because there is evidence from several families to show that it is the remains of the basal section of R_4, which had been pectinate on R_{2-3}. Dr. Philip has sent me a specimen of the Nearctic *Tabanus productus* Hine, in which this vein is complete on one wing and almost so on the other. Development of the appendix is variable, but it has a definite taxonomic usefulness, provided its limitations are appreciated.

The presence of setulae on the basicosta (Fig. 6C) is the essential character separating Tabanini from Diachlorini (Fig. 6B). It tends to break down in the Neotropical and Holarctic regions, but has been completely constant in all the Australian material I have examined. Setulae on other veins are not so reliable. Those on *Sc* have a limited usefulness in that they are always present, at least on the lower surface, in Tabaninae, always absent in Pangoniinae, and present or absent in Chrysopinae. Others, including the row which is sometimes conspicuous on the upper surface of Cu_1, are extremely variable, even within species, and I have not been able to make any practical use of them in the Australian fauna.

The squames and halteres have only occasionally proved to be useful, so they are omitted from most of the descriptions.

(e) Genitalia

The method of dissection is as follows. The terminal segments are snipped off with a pair of fine scissors, sacrificing enough of the abdomen to ensure that the retracted genital segments are not cut through, or crushed. The detached portion is then boiled in 10 per cent. KOH for about 15 min, passed through water, two changes of glacial acetic acid, two changes of clove oil (10-15 min at each step), and mounted in balsam. Dissection is done under a Greenough binocular microscope in the second change of oil. The basal segments are removed, and usually discarded. In the male, the 9th tergite and parts attached to it are dissected off, and the residual tissues and tracheae cleaned out from both dorsal and ventral parts, before mounting them between cover-slips cemented to a piece of card. In the female, the 8th sternite is dissected away from the parts that overlie it, the genital fork and spermathecal ducts being left attached either dorsally or ventrally, whichever may prove convenient in the individual dissection. The mounted parts are attached to the pin carrying the insect from which they were dissected.

The structures have been described in an earlier paper (Mackerras 1955a, pp. 444-7), and their details are shown in Figures 7 and 8, which are partly from that paper. Their significance in classification will be discussed in the next section, and it need only be noted here that they do not usually help in discriminating between genera or species. There are a few exceptions, however, and these are occasionally so useful (for

example, the difference in shape of the 8th sternite of the female between *Scaptia maculiventris* (Westw.) and the closely related *S. testaceomaculata* (Macq.) that dissection, at least of Pangoniinae, would always seem to be justified.
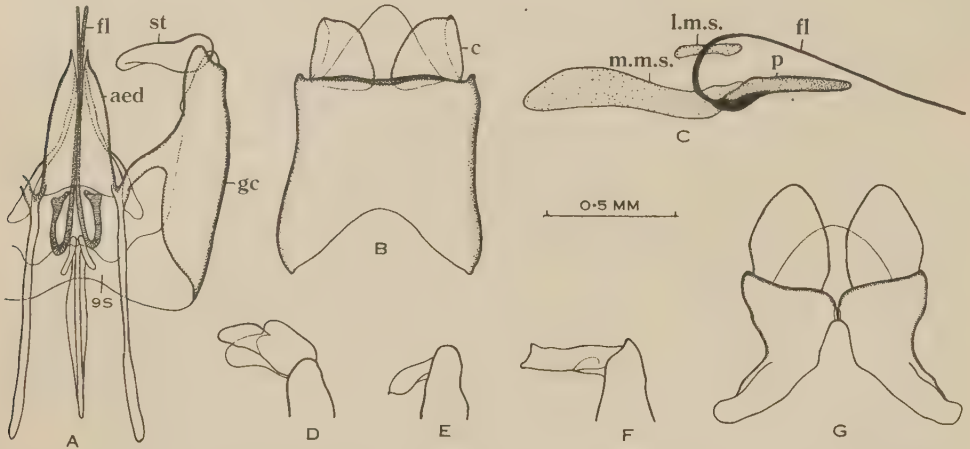
Fig. 7.—*A-C, Scaptia (Scaptia) patula* (Walk.), Scionini: *A*, male genitalia: 9S, 9th sternite; *aed*, aedeagus; *fl*, flagellum; *gc*, gonocoxite; *st*, style. *B*, 9th tergite and associated parts: *c*, cerci. *C*, lateral view of penis (*p*), flagellum (*fl*), and muscle struts (*l.m.s., m.m.s.*). *D-F*, style of: *D, Austroplex goldfinchi* Mack., Pangoniini; *E, Mesomyia (Lilaea) fuliginosa* (Tayl.), Chrysopinae; *F, Cydistomyia doddi* (Tayl.), Tabaninae. *G*, terminal segments of *C. doddi*, showing divided 9th tergite. All figures at same magnification.

VI. Classification

The classification of the family into subfamilies and tribes is based on two sets of characters, genitalic, which are precise so far as they go, and external, which are more variable and more liable to be obscured by convergent evolution (Mackerras 1954, 1955a). The divisions that can be made on genitalic characters are shown in the following tabular statement, which also indicates the relationships between the groups.

A.   Ninth tergite entire, large and shield-like in ♂, a transverse bar in ♀; caudal
     ends of spermathecal ducts of ♀ without expansions ....PANGONIINAE
     a. Style of ♂ bifid ....Pangoniini
     b. Style of ♂ simple ....Scionini
B.   Ninth tergite divided, the halves approximated in ♂, widely separated triangular
     plates in ♀.
     a. Style of ♂ pointed; caudal ends of spermathecal ducts of ♀ without
        expansions ....CHRYSOPINAE
     b. Style of ♂ truncate; caudal ends of spermathecal ducts of ♀ with mush-
        room-shaped expansions ....TABANINAE

Transitional forms between tribes have not been found in Australia, and a key based entirely on external characters can therefore be

used with reasonable confidence. The only difficulty is to distinguish between some Pangoniini and Bouvieromyiini. An attempt has been made to reduce this by bringing the Pangoniini out twice, but doubtful specimens should always be dissected, and their genitalic characters checked from the tabular summary and the definitions in later Parts of this series.
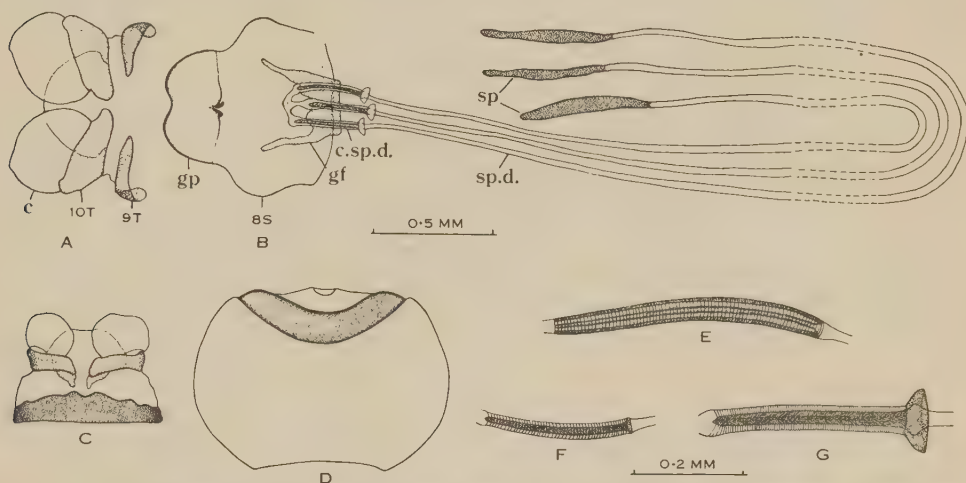
Fig. 8. —*A-B*, female genitalia of *Cydistomyia doddi* (Tayl.): *A*, terminal segments: 9*T*, 9th tergite; 10*T*, 10th tergite; *c*, cerci. *B*, 8th sternite and associated parts, viewed from above: 8*S*, 8th sternite; *gp*, anterior gonopophyses; *gf*, genital fork; *c.sp.d.*, caudal ends of spermathecal ducts (*sp.d.*); *sp*, spermathecae. *C*, terminal segments of *Ectenopsis* (*Ectenopsis*) *vulpecula* (Wied.), ♀, showing undivided 9th tergite. *D*, 8th sternite of *Philoliche neocaledonica* (Mégnin), ♀, New Caledonia, showing wide, chitinized distal edge characteristic of the tribe. *E-G*, caudal ends of spermathecal ducts of: *E*, *Scaptia* (*Pseudoscione*) *maculiventris* (Westw.), Pangoniinae; *F*, *Mesomyia* (*Pseudotabanus*) *distincta* Ric., Chrysopinae; *G*, *Cydistomyia sanguinaria* (Big.), Tabaninae.

KEY TO SUBFAMILIES AND TRIBES OF TABANIDAE IN AUSTRALIA

1. Hind tibiae without spurs; ocelli absent or rudimentary; 3rd antennal segment with a basal plate and a style of 4 (rarely 3) annuli ....TABANINAE, 2
    Hind tibial spurs usually conspicuous, sometimes small, rarely absent; ocelli well developed 3

2. Basicosta covered with setulae similar to those on costa ....Tabanini
    Basicosta bare, contrasting with costa ....Diachlorini

3. Third antennal segment more or less subulate, composed of 8 to 6 (rarely 5) annuli ....PANGONIINAE, 4
    Third antennal segment with basal plate and a style of 4 (occasionally fewer) annuli 5

4. Eyes densely hairy;* vein R_4 usually without appendix; cell R_5 often closed; usually rotund species ....Scionini
    Eyes usually bare, at most inconspicuously hairy; vein R_4 with appendix; cell R_5 widely open; usually more slender species ....Pangoniini (pt.)

* Except ♀ of *Scaptia conspicua* (Ric.)

5.   Vein R_4 with appendix; frons of ♀ usually wide, and rarely with a small
        callus ....Pangoniini (pt.)
      Vein R_4 rarely with appendix; frons of ♀ usually medium to narrow, and almost
        always with a well developed callus ....`................CHRYSOPINAE, 6
6.   Slender species; antennae much longer than antero-posterior thickness of head,
        1st segment more than twice as long as wide ....Chrysopini
      Usually normal, diachlorine-like species; antennae not longer than antero-posterior
        thickness of head, 1st segment little longer than wide ....Bouvieromyiini

Tribe PHILOLICHINI Mackerras

This tribe of Pangoniinae has not been included in the table or
key, because it has not been found in Australia. It may be recognized
by the following characters. Stoutly built species; eyes bare; ocelli
absent; antennae subulate, 8-annulate; proboscis slender, with unex-
panded labella; vein R_4 with appendix; 8th sternite of ♀ with widely
separated gonopophyses, and its distal edge forming a rolled, relatively
strongly chitinized projection (Fig. 8D); style of ♂ hypopygium simple,
pointed.

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VIII. BIBLIOGRAPHY OF AUSTRALIAN TABANIDAE

This list contains all the references to Australian species that I have been able to discover. It seems more useful to present it here as a single bibliography, rather than break it up (with repetition of many of the references) among the several Parts of the series.

Most of the citations have been checked from the originals, but some of the older and rarer works are not available in Brisbane. I have depended for these on Ferguson's set of transcripts of the original descriptions, which he left with me when he died, and have used Musgrave's (1932) bibliography as a check on dates and titles. For this reason, the pagination of Macquart's "*Diptères exotiques..*" as issued separately, has been used, rather than the original in *Mém. Soc. Sci...
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THE TABANIDAE (DIPTERA) OF AUSTRALIA. I
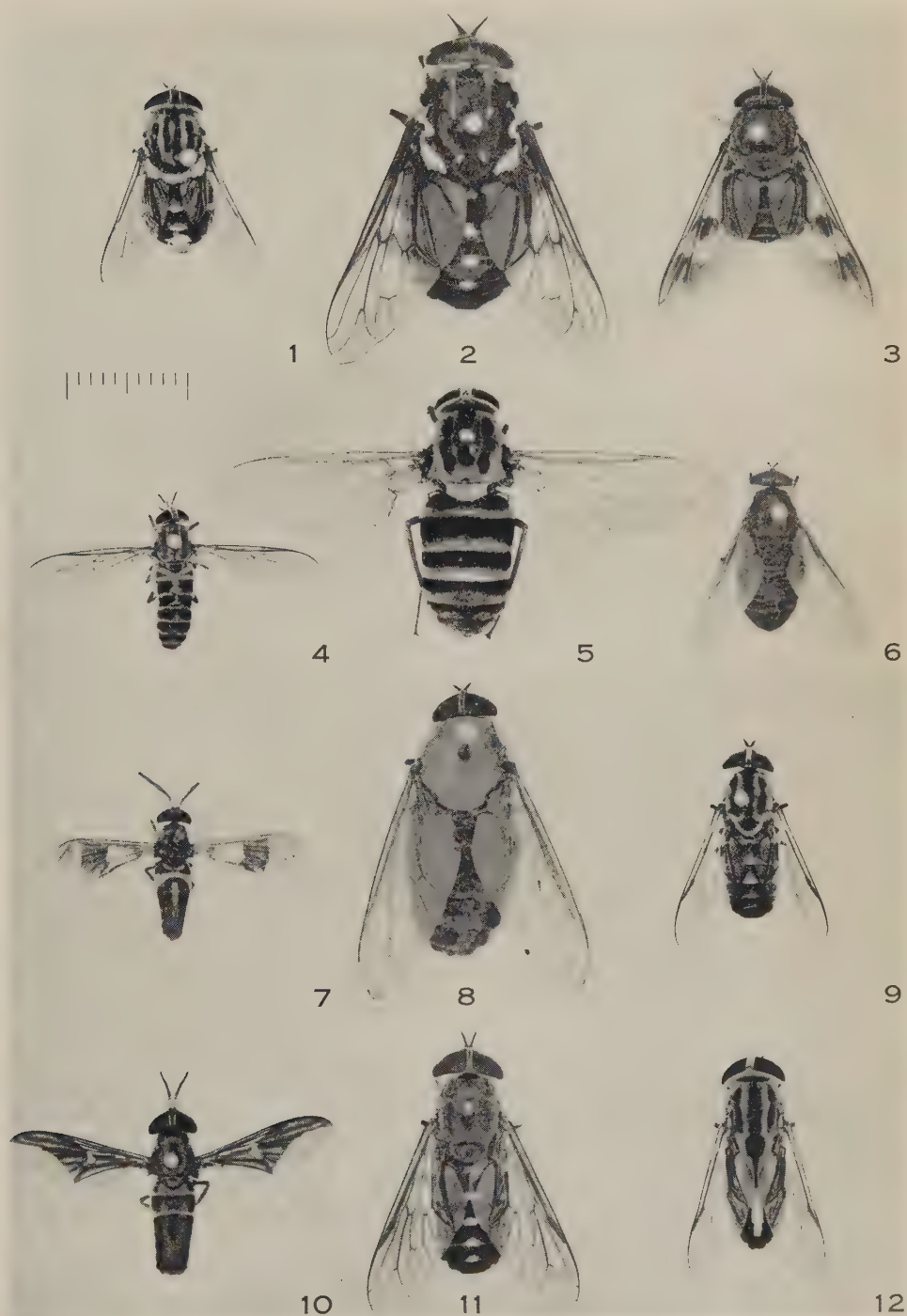
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EXPLANATION OF PLATE 1

Representative Australian Tabanidae, females. The scale is in millimetres. Photographs by M. J. Mackerras

Figs. 1-6.—Pangoniinae: 1, *Scaptia (Scaptia) aurata* (Macq.); 2, *Scaptia (Scaptia) guttata* (Don.); 3, *Scaptia (Pseudoscione) lasiophthalma* (Macq.); 4, *Ectenopsis (Ectenopsis) australis* Ric.; 5, *Austroplex chrysophilus* (Walk.); 6, *Ectenopsis (Parasilvius)* sp. (W.A.).

Figs. 7-9.—Chrysopinae: 7, *Chrysops australis* Ric.; 8, *Pseudopangonia australis* Ric.; 9, *Mesomyia (Pseudotabanus) queenslandi* Ric.

Figs. 10-12.—Tabaninae: 10, *Paracanthocera australis* (Ric.); 11, *Cydistomyia doddi* (Tayl.); 12, *Tabanus strangmani* Ric.

THE TABANIDAE (DIPTERA) OF AUSTRALIA

II. SUBFAMILY PANGONIINAE, TRIBE PANGONIINI

By I. M. Mackerras*

(Manuscript received July 9, 1956)

Summary

The Australian Pangoniini include the most primitive known Tabanidae. Most are low-flying insects, which do not suck blood. They show progressive reduction in mandibles of the female, divisions of the third antennal segment, and hind tibial spurs. Their principal distribution is east coastal, from Torres Strait to southern New South Wales; there is a secondary centre of evolution in Western Australia; they are not known from Tasmania.

Eighteen species are recognized, distributed among seven genera and subgenera, as follows: *Austroplex*, 3; *Ectenopsis* (*Ectenopsis*), 4; *Ectenopsis* (*Parasilvius*), 4; *Ectenopsis* (*Leptonopsis*), 2; *Caenoprosopon*, 4; *Therevopangonia*, 1.

Three new species are described from Western Australia: *Ectenopsis* (*?Ectenopsis*) *occidentalis*, ♂; *Ectenopsis* (*Parasilvius*) *fusca*, ♂, ♀; *Ectenopsis* (*Leptonopsis*) *norrisi*, ♂.

INTRODUCTION

The flies to be described in this Part are an inconspicuous element in the Australian tabanid fauna, and most are unlike normal Tabanidae in appearance and behaviour, but they are of particular interest to the student of evolution and zoogeography. It seems possible that they have been adversely affected by the advance of human settlement, because most of the specimens I have seen were collected more than 30 years ago.

Definitions in this and subsequent Parts of this series are based on Australian material; they are not necessarily fully applicable in other countries. The references cited are listed in the bibliography in Part I of this series (pp. 401-406).

Subfamily **PANGONIINAE**

Ninth tergite an undivided, chitinous shield in ♂; a single transverse bar in ♀. Ocelli well developed. Antennae little if at all longer than the antero-posterior diameter of the head; 1st and 2nd segments short; 3rd usually subulate and 6- to 8-annulate. Hind tibiae nearly always with paired apical spurs. Vein *Sc* bare above and below. Style of ♂ hypopygium single or bifid, never truncate. Caudal ends of spermathecal ducts of ♀ without mushroom-like expansions.

Two tribes occur in Australia, Pangoniini and Scionini.

* Queensland Institute of Medical Research, Brisbane.

Tribe PANGONIINI

Style of ♂ hypopygium bifid. Eyes usually bare or with inconspicuous hairs, occasionally densely hairy in ♂. Frons of ♀ sometimes with a callus. Third antennal segment variable; subulate, or distinctly swollen at base; usually with 6-8 annuli, occasionally reduced to 4; sometimes the basal 3 or 4 more or less fused and indistinct. Palpi generally sabre-shaped or awl-shaped in both sexes. Hind tibial spurs variable, sometimes very small, occasionally not detectable. Vein R_4 with appendix.

The Australian genera belong to the more primitive division of the tribe (Group 1 of Mackerras 1955a, p. 459), which is characterized by:

Cell R_5 open; proboscis not much, if at all, longer than head height, usually stout; labella expanded, usually large and soft; habitus not *Pangonius*-like.

Evolution

Ectenopsis (s.s.) is the most primitive tabanid known to me. It probably differs from the original ancestors of the Tabanoidea in little more than modification of the male hypopygium (development of flagella and a bilobed style), reduction of the cerci of the female to a single segment, loss of most of the basal section of R_4, closure of cell Cu_2, development of squames, and partial reduction of the mandibles of the female. Its larvae and pupae do not seem to be as primitive as the adults, but it is difficult to assess values when so few forms are known.

Several anatomical trends can be seen in the Australian genera, and some of them are particularly interesting, because they demonstrate that important taxonomic characters do not necessarily evolve only once; they may appear and be selected repeatedly, even when their adaptive significance is not apparent to the taxonomist.

One change which does seem obviously related to mode of life is reduction of the mouthparts of the female. Most Tabanoidea have lost the mandibles, and the Australian Pangoniini (Fig. 1) illustrate the steps in the process. The mandibles of *Austroplex* seem to be somewhat thin and flexible, but are otherwise normal; they are progressively shorter and thinner in the subgenera *Parasilvius* and *Ectenopsis;* and cannot be detected in *Caenoprosopon* and *Therevopangonia*. In *Caenoprosopon*, the base of the maxilla tends to become separated from its palp and applied more closely to the labrum.

It has already been noted (Mackerras 1954) that *Ectenopsis* has the only form of palpi which could have been ancestral to that of generalized Chrysopinae and Tabaninae. Another primitive feature of the group is the lack of significant sexual dimorphism in the palpi of all the Australian genera except *Austroplex*.

Compaction and reduction of the 3rd antennal segment lead almost precisely to the same end result as has been achieved in Chrysopinae and Tabaninae, and we can see similar progressive reduction in the hind

tibial spurs, with apparently complete extinction in some specimens of
Caenoprosopon, a fact which led Kröber (1931) to suggest excluding
Demoplatus (= *Caenoprosopon*) from the Opisthacanthae. Further
parallelism is shown in the occasional development of a callus in Pan-
goniini, usually approximating to the elongate form which is common in
generalized Bouvieromyiini and Diachlorini.
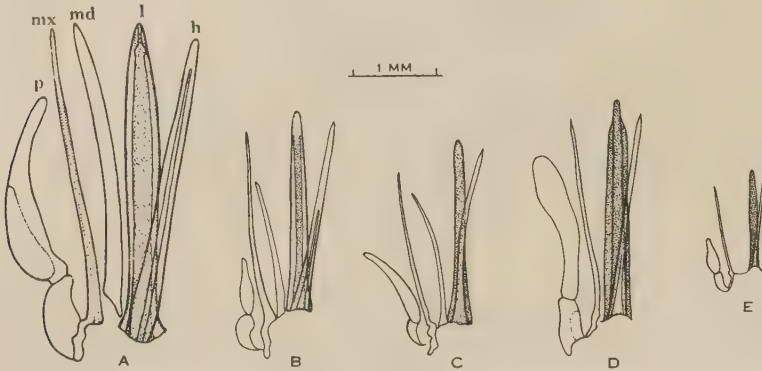
Fig. 1.—Mouthparts of females of: *A, Austroplex chrysophilus* (Walk.) ; *B, Ectenopsis*
(*Parasilvius*) *fulva* Ferg.; *C, Ectenopsis* (*Ectenopsis*) *angusta* (Macq.); *D, Caeno-
prosopon trichocerus* (Big.) ; *E, Therevopangonia insolita* Mack. *l*, labrum-epipharynx;
h, hypopharynx; *md*, mandible; *mx*, maxilla; *p*, palp. Drawn from ventral side, with
labium removed.

I have not used the colour of the eyes in the definitions of genera or
species, but the findings on relaxed specimens may be recorded here,
because they show more variation than might be expected in such a
primitive group. The eyes are dark brown to blackish (sometimes with
a hint of green in the black) in the species of *Austroplex, Caenoprosopon,*
and *Therevopangonia,* except for the female of *C. trichocerus,* in which
they are light reddish brown. They differ considerably in the subgenera
of *Ectenopsis.* All the species of *Parasilvius* have green eyes in both
sexes, including the dark-bodied *E. (P.) fusca.* In *E. (Leptonopsis)*
vittata, the male has green eyes, but the female has the upper facets
blackish and the lower dark brown, the colours being separated by a
just perceptible, oblique line. Hardy (1939) described the eyes of a
species of the subgenus *Ectenopsis* (probably *angusta*) from fresh
specimens as green, with a red band, which does not reach the lateral
margin, and is narrow in the male, wider in the female. I have been able
to see the red band in only a few relaxed males, but at least traces of it
(oblique, and purple rather than red) are present in females of all the
species, and it is conspicuous in some. The ground colour has varied from
dark brown or blackish to green. I suspect that these variations may be
due to imperfections in the method, rather than to differences within the
subgenus.

The specialized male genitalia, remarkably constant throughout the tribe, prove that the Pangoniini, as we know them today, are not surviving ancestors of the Chrysopinae and Tabaninae. Nevertheless, there is no doubt that all three were derived from common stock. The Pangoniini evolved more slowly in most ways, and they show in still plastic form the trends which have become stabilized into major taxonomic characters in the other two groups.

Fig. 2.—Distribution of Australian Pangoniini. A, ● Ectenopsis (Ectenopsis), ○ Ectenopsis (Leptonopsis); B, Ectenopsis (Parasilvius); C, ● Caenoprosopon, ○ Therevopangonia; D, Austroplex.

It is difficult to write about the evolution of the genera themselves without more knowledge of their South American relatives. I suspect that something very like the subgenus Ectenopsis occurred in both countries, and that parallel evolution has led, for example, to independent local development of the Australian Parasilvius, the New Zealand Paranopsis, and the Chilean Chaetopalpus, all of which have a compacted 3rd antennal segment. Caenoprosopon and Therevopangonia probably evolved here in Australia, but Austroplex has wider relationships. It is connected by genitalic characters with Ectenopsis on the one hand, and by external

characters with the American *Esenbeckia* on the other. It cannot be far removed from the ancestral type, from which the more specialized Group 2 evolved.

Distribution

The material available is insufficient for a detailed analysis of the distribution of the tribe in Australia, but the basic pattern is evidently similar to that of the more abundant genus *Scaptia*.

Five of the seven genera and subgenera are found in eastern Australia (Fig. 2). Nearly all the species are coastal, and there are few records from high country and west of the Dividing Range. *Ectenopsis* (s.s.), *Caenoprosopon*, and *Austroplex* have the widest range, *Ectenopsis* extending from Moa I. in Torres Strait to the National Park south of Sydney, *Caenoprosopon* from Cairns to Illawarra, and *Austroplex* from Herberton to Sydney. There is an apparently reliable record of *Austroplex* from Western Australia and a doubtful one of *Caenoprosopon* from South Australia; but *Ectenopsis* is replaced by other subgenera in the southern and western part of the continent. The subgenus *Parasilvius* is predominantly southern (Victoria, South Australia, and Western Australia), but one species (*hamlyni*) has been found in southern Queensland and western New South Wales. As in *Scaptia*, there is a subsidiary centre of evolution in Western Australia, represented by the subgenus *Leptonopsis* and the curious little *Therevopangonia*. There is no indication of a northern centre, nor of eastward dispersal from the western centre.

The seasonal distribution is not striking. *Parasilvius* shows something of the seasonal features of other southern groups, in that adults have been taken in the summer in southern localities and in the spring in more northern ones. *Leptonopsis* has also been collected in the spring, but nearly all the records of other members of the tribe are from November to January, with a numerically small extension to March. Miss English, who had a breeding ground near Sydney under observation for some time, found that adults of *Ectenopsis* (*Ectenopsis*) *angusta* emerged during December and January.

Habits and Life-history

Very little has been recorded of the habits of these flies. There is no record that any of them sucks blood, and it seems evident from the structure of the mouthparts that only the species of *Austroplex* might be able to do so. Most specimens have been collected on shrubs, bracken, and low vegetation generally, only a few on *Leptospermum* flowers, and a few on *Bursaria*.

The life-history of *E. (E.) angusta* has been described by English (1953), and is the only one known in the tribe. Larvae and pupae were found within a few inches of the surface, in black, sandy loam, which was usually moist, but well drained and not at all swampy. Some larvae

were kept alive in captivity for nearly 2 years, so it would seem either that the life-history is prolonged or that the larvae are adapted to withstand long periods of adversity. The larvae are peculiar in shape, being
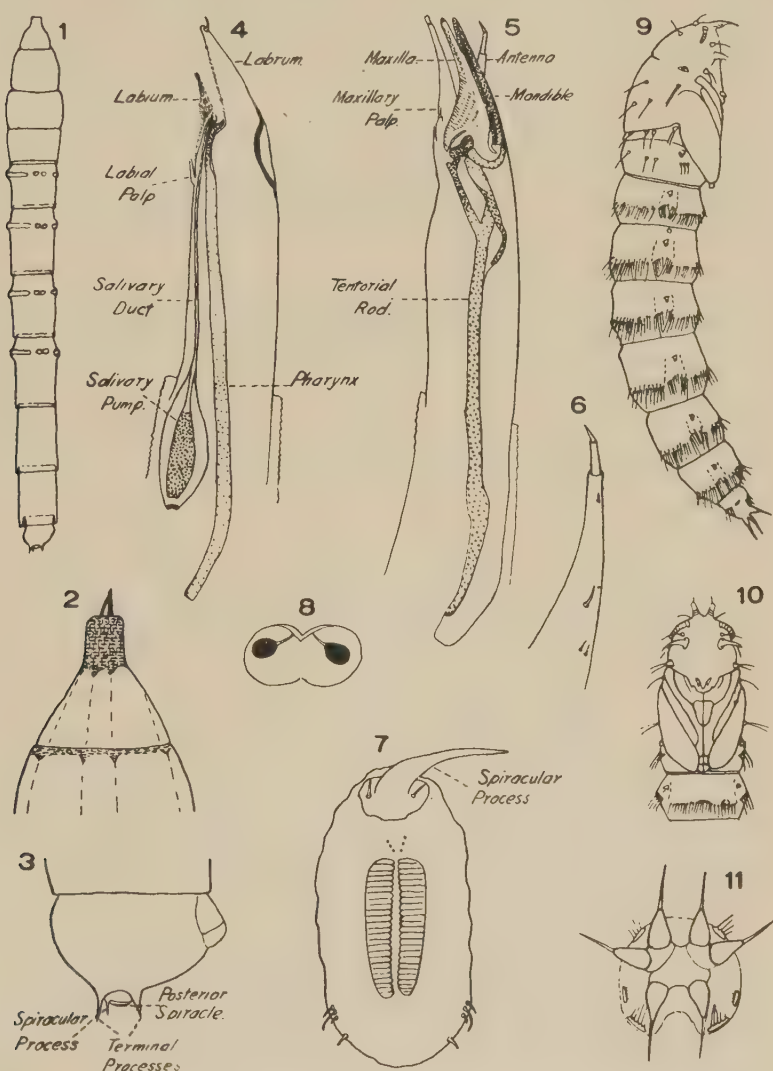
Fig. 3.—Larva and pupa of *Ectenopsis* (*Ectenopsis*) *angusta* (Macq.), from English (1953) by permission of the Linnean Society of New South Wales. 1-8, Larva: 1, lateral view; 2, lateral view of anterior end; 3, lateral view of posterior end; 4, 5, mouthparts in longitudinal section; 6, antenna; 7, spiracular area and posterior spiracle; 8, Graber's organ. 9-11, Pupa: 9, lateral view; 10, ventral view of anterior end; 11, posterior end seen from behind.

long, slender, and unlike any other described tabanid, but the pupae are more normal, and have a typical, 6-rayed aster (Fig. 3).

Key to Genera and Subgenera of Australian Pangoniini

1.   Large, robust species; 3rd antennal segment swollen at base, 8-annulate; frons of ♀ with a callus ....*Austroplex* Mack.
   Smaller, usually more slender species; 3rd antennal segment either not swollen at base, or with fewer than 8 annuli; frons of ♀ usually without callus 2

2.   Very small, bristly, therevid-like species, with very wide frons, shining sublateral patches on subcallus, and broadened, 4-annulate 3rd antennal segment ......
   ....*Therevopangonia* Mack.
   Larger, smoother species, with subcallus entirely tomentose, and 3rd antennal segment 5- to 8-annulate 3

3.   Subcallus and face of ♀ strongly projecting, giving a distinctive profile (Fig. 8); 3rd antennal segment of both sexes much narrower than 2nd, usually 8- or 7-annulate; palpi of both sexes long, typically sabre-shaped ....
   ....*Caenoprosopon* Ric.
   Subcallus and face of ♀ normal, but face sometimes triangularly produced in profile; 3rd antennal segment usually little if at all narrower than 2nd; palpi shorter, subcylindrical, or awl-shaped ....*Ectenopsis* Macq. 4

4.   Third antennal segment swollen at base, and with basal 4 annuli more or less fused; palpi less than half the length of the shaft of the proboscis; eyes perceptibly hairy; more broadly built species ......Subgen. *Parasilvius* Ferg.
   Third antennal segment slender, distinctly 8- or 7-annulate; palpi long or short; eyes bare; more slender species 5

5.   Face triangularly produced in profile; 3rd antennal segment about half as wide as 2nd; palpi much less than half the length of the shaft of the proboscis; labella small ....Subgen. *Leptonopsis* Mack.
   Face truncate in profile; 3rd antennal segment little narrower than 2nd; palpi longer than half the shaft of the proboscis; labella large ....
   ....Subgen. *Ectenopsis* Macq.

Genus AUSTROPLEX Mackerras

Corizoneura auct., pt., nec Rondani, 1863. (The true *Corizoneura* is a synonym of *Philoliche*.)

Buplex Ferguson and Hill, 1922, pp. 248, 249; Ferguson 1924, p. 256, 1926a, p. 294; nec Austen, 1920. (*Buplex* Aust. is an African genus of Philolichini.)

Austroplex Mackerras, 1955a, p. 466. Genotype *Austroplex goldfinchi* Mackerras, 1955, Queensland, by original designation.

Female

Large (16-22 mm), smooth-bodied, robust species, with large, bare eyes. Frons of medium width (index about 3), parallel or slightly diverging, tomentose, and with an elongate callus; ocellar tubercle prominent. Subcallus normal, tomentose, without hairs. Parafacials narrow; face convex. Antennae with 3rd segment distinctly expanded basally, normally 8-annulate, with the last annulus long and slender, and usually with the basal annuli rather poorly defined. Palpi long, sabre-shaped or broadened basally, and with a lateral bare area. Proboscis about equal to head height, stout, with large, expanded, unchitinized labella. Hind tibial spurs strong. Hypopygium with gonopophyses conical; caudal ends of spermathecal ducts variable, sometimes delicate, sometimes moderately chitinized.

Male

Similar to ♀. Eyes bare, contiguous, upper facets distinctly enlarged and differentiated from the lower. Palpi with 1st segment swollen, and 2nd subcylindrical, tapering to a blunt point, more hairy than in ♀. Hypopygium normal; aedeagus with large flagella; both lobes of style rounded at tip, the dorsal considerably smaller than the ventral.

To be distinguished from other genera of the tribe by size and robust build, and by the form of the 3rd antennal segment and palpi. Females of the *guttata* group of *Scaptia* have palpi of somewhat similar shape, but are easily distinguished by their densely hairy eyes, absence of a callus, and different venation.

Nothing is recorded of the behaviour or life history of the species. Nearly all the specimens in collections are old, as Ferguson and Hill (1922) remarked, and it would seem that these insects are now much rarer than they used to be. The distribution of the genus is shown in Figure 2*D*.

As the old name *Corizoneura* was used rather loosely, I append a list of the Australian species which have been included in it at one time or another:

C. *angusta* (Macq.) = *Ectenopsis* (*Ectenopsis*) *angusta* (Macq.)
C. *angusta* Bigot = *Ectenopsis* (*Ectenopsis*) *angusta* (Macq.)
C. *anthracina* (Macq.) = *Scaptia* (*Scaptia*) *subcana* (Walk.)
C. *berylensis* Ric. = *Scaptia* (*Scaptia*) *berylensis* (Ric.)
C. *bigoti* End. = *Ectenopsis* (*Ectenopsis*) *angusta* (Macq.)
C. *brevipalpis* (Macq.) = *Austroplex brevipalpis* (Macq.)
C. *chrysophila* (Walk.) = *Austroplex chrysophilus* (Walk.)
C. *conspicua* Ric. = *Scaptia* (*Pseudoscione*) *conspicua* (Ric.)
C. *dives* (Macq.) = *Scaptia* (*Scaptia*) *auriflua* (Don.)
C. *fulva* (Macq.) = *Austroplex brevipalpis* (Macq.)
C. *hamlyni* (Tayl.) = *Ectenopsis* (*Parasilvius*) *hamlyni* (Tayl.)
C. *kurandae* Tayl. = *Mesomyia* (*Pseudotabanus*) *queenslandi* Ric.
C. *nigricornis* (Bigot) = *Scaptia* (*Scaptia*) *plana* (Walk.)
C. *nigrosignata* (Thom.) = *Austroplex chrysophilus* (Walk.)
C. *rubiginosa* Bigot = *Ectenopsis* (*Ectenopsis*) *angusta* (Macq.)
C. *rufovittata* (Macq.) = *Austroplex chrysophilus* (Walk.)
C. *trichocera* Bigot = *Caenoprosopon trichocerus* (Bigot)

KEY TO SPECIES OF THE GENUS AUSTROPLEX

1. Entirely fawn-yellow species; without darker markings on thorax or abdomen
    ....*brevipalpis* (Macq.)
    Somewhat darker species; scutum and abdomen with dark brown to black markings 2

2. More robust species; scutum with well-defined dark vittae; dark bands on abdomen broad ....*chrysophilus* (Walk.)
    Not such robust species; scutum with dark markings behind suture only; abdominal bands narrower ....*goldfinchi* Mack.

AUSTROPLEX BREVIPALPIS (Macquart)

Pangonia brevipalpis Macquart, 1847, p. 8; Walker 1848, p. 144, 1854, p. 134. Type ♂, from Australia, stated to be in the Paris Museum.

Corizoneura brevipalpis (Macquart). Ricardo 1900a, p. 113; Froggatt 1911, p. 12; Surcouf 1921, p. 134.

Buplex brevipalpis (Macquart). Ferguson 1926a, pp. 294, 304.

Pangonia fulva Macquart, 1850, p. 19. Type ♂, from east coast of New Holland, stated to be in the Paris Museum; allotype ♀, designated by Ricardo 1915b, stated to be in the German Entomological Museum, Berlin. Synonymy by Ferguson 1926a, p. 304.

Corizoneura fulva (Macquart). Ricardo 1900a, pp. 113, 120, 1915b, p. 36; Froggatt 1911, p. 12; Taylor 1917b, p. 517, 1918, p. 61; Surcouf 1921, p. 134; Ferguson 1922, p. 184; Enderlein 1925, p. 271.

Material examined.—3 ♂ ♂, 1 ♀.

A large, light yellowish brown species, with faintly greyish wings slightly tinged with brown anteriorly, and uniformly yellowish legs. Length: 16-17 mm.

Female

Head.—Frons slightly diverging, with creamy fawn tomentum, and short, inconspicuous, yellowish hairs; callus light brown, elongate, extending from the ocellar triangle, widening in the middle, and tapering to a point just above the subcallus. Subcallus cream with a pale fawn tint. Parafacials similar, with some inconspicuous pale hairs on their lower part; face slightly darker, with brownish yellow hairs in the median area and paler ones laterally. Antennae with basal segments orange-yellow, with a creamy overlay and brownish orange hairs; 3rd missing. Palpi orange-yellow, as long as shaft of proboscis, narrow, with an elongate bare area, and with dull cream hairs on 1st segment, brownish orange on 2nd. Beard short, dull cream.

Thorax.—Scutum and scutellum light yellowish brown, with indications of somewhat darker, narrow, median and dorsocentral lines; hairs on disc and margins golden to creamy golden, somewhat darker laterally in front of wing root. Pleurae light brownish yellow, with a faint creamy overlay, and with dull yellowish hairs over most of the sclerites, but pale yellowish cream ones on upper mesopleural tuft and between the coxae.

Legs.—Orange-yellow, with orange hairs.

Wings.—Faintly grey, with a yellowish tinge at extreme base; costal cell light brown; veins pale yellowish to light brown.

Abdomen.—Concolorous with scutum, the basal segments somewhat lighter, and the whole covered with golden orange hairs, which become more creamy gold at lateral margins. Venter light yellowish brown with a greyish overlay, and with golden hairs, strongest at the apical edges of the sternites.

Male (Plate 1, Fig. 1)

Similar to ♀, but with more conspicuous, rich golden hairs on thorax and abdomen. Third antennal segment a little paler than the basal segments, shaped as in *A. chrysophilus*. Wing veins pale yellow, costal cell yellowish rather than brown, and a tendency for yellowish suffusion along the veins.

Distribution.—QUEENSLAND: Herberton, 3700 ft, Dec., Dodd (Ricardo 1915b); Bribie I., Nov., Hacker; Stradbroke I., Dec., Hacker. NEW SOUTH WALES: Hunter R. (Ricardo 1915b); Sydney (no other data). WESTERN AUSTRALIA: Waroona, Mar., G. F. Berthoud. This is the female described above. It is in the Froggatt Collection in the Division of Entomology, C.S.I.R.O.; the locality label seems authentic.

AUSTROPLEX GOLDFINCHI Mackerras

Corizoneura chrysophila, ♂, Ricardo 1915b, p. 36, nec Walker, 1848, ♀. It is clear from the note: "In the male only two short ones" (i.e. brown stripes) "at base of thorax are visible", that she misallied the sexes, as I did also until a female of this species was received.

Austroplex goldfinchi Mackerras, 1955a, p. 467. Holotype ♀ and allotype ♂, from Yeppoon, Queensland, November, in the School of Public Health and Tropical Medicine, University of Sydney.

Material examined.—4 ♂ ♂, 2 ♀ ♀.

A large, yellowish fawn species; scutum with dark brown sublateral patches behind suture; abdomen with dark brown basal bands, which are less than half the width of the tergites; wings pale greyish with a hint of yellow; legs uniformly yellow. Length: 16-20 mm.

Female

Head.—Frons parallel, somewhat wrinkled longitudinally, covered with creamy fawn tomentum, except for a small, elongate, greyish brown callus on its lower half; there is a small group of very short but strong dark hairs on either side of the callus, otherwise the frons is without hairs. Subcallus concolorous with frons. Parafacials similar, with a few pale hairs near lower margin; face darker, with a narrow zone of brown hairs extending across the middle. Antennae with basal segments creamy, with rich brown hairs; 3rd orange-yellow. Palpi wider than in *A. brevipalpis*, nearly as long as proboscis, creamy, with brown hairs except for the brownish orange bare area. Beard short, light brown to yellowish cream.

Thorax.—Scutum yellowish fawn, with brown hairs; pronotal lobes and anterior margin paler, almost creamy yellow, and indications of a pair of short pale creamy stripes on either side of the median line anteriorly. There is an inconstant, elongate, narrow, dark brown patch in the median line at about level of suture, and a larger, elongate, oval, dark brown patch lateral to the almost invisible dorsocentral lines behind the suture. Scutellum yellowish fawn, with dull golden hairs. Pleurae yellowish fawn, somewhat variable in colour, and with brownish gold to rich brown hairs.

Legs.—Yellow, with golden to brownish gold hairs.

Wings.—Faintly tinged with grey, costal cell not appreciably darkened; veins yellowish to light yellowish brown.

Abdomen.—Bright yellowish fawn, with a dark brown basal patch on either side of the median line on 1st tergite, and conspicuous black or blackish brown bands on remaining tergites; these bands are not more than half the width of the tergite in the median area, but tend to widen slightly laterally; hairs black on the dark areas, bright golden on the pale parts. Venter similar to dorsum, but darker colour more diffuse, and brown rather than black.

The second ♀ has a slightly diverging, more yellowish frons, orange face, and orange hairs on basal antennal segments and over greater part of scutum; the marginal scutal hairs are orange-brown.

Male

Similar to ♀, but the dark sublateral scutal marking behind the suture is sometimes inconspicuous, and the abdominal bands may be interrupted in the median line.

Distribution.—QUEENSLAND: Mackay, A. Marriage; Yeppoon, Nov., Goldfinch; Burpengary, 1904, T. L. Bancroft (Ricardo 1915*b*).

AUSTROPLEX CHRYSOPHILUS (Walker)

Tabanus chrysophilus Walker, 1848, p. 155. Type ♀, from Australia, in the British Museum (Natural History). Not a homonym of *Pangonia chrysopila* Macquart, 1834, Africa, as inadvertently suggested by Ricardo 1900*a*, p. 121.

Corizoneura chrysophila (Walker). Ricardo 1900*a*, pp. 113, 120, 1915*b*, p. 36; Froggatt 1911, p. 12; Ferguson 1916, p. 205, 1922, p. 184; Ferguson and Hill 1922, p. 248; Taylor 1918, p. 61; Surcouf 1921, p. 134; Enderlein 1925, p. 271.

Buplex chrysophilus (Walker). Ferguson 1926*a*, p. 294.

Pangonia rufovittata Macquart, 1850, p. 19. Type ♀, from "Tasmanie",* in the British Museum (Natural History). Synonymy by Ferguson and Hill 1922, p. 248.

Corizoneura rufovittata (Macquart). Ricardo 1900*a*, p. 113; Froggatt 1911, p. 12; White 1915, p. 18; Surcouf 1921, p. 134; Enderlein 1925, p. 271.

Pangonia aurofasciata Jaennicke, 1868, p. 327. Type ♀ from Australia, location not stated. Synonymy by Ricardo 1900*a*, pp. 113, 120.

Pangonia nigrosignata Thomson, 1868, p. 451. Type ♀, from Sydney, N.S.W., in the Stockholm Museum. Synonymy by Ricardo 1915*b*, p. 36. I concur, from examination of the type, which was sent to Dr. S. J. Paramonov at Canberra for study.

Corizoneura nigrosignata (Thomson). Ricardo 1900*a*, p. 113; Froggatt 1911, p. 12; Enderlein 1925, p. 271.

Material examined.—13 ♀ ♀.

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* Most, if not all, the Diptera described by Macquart in his 4th Supplement as from Tasmania actually came from the east coast of the mainland (Ferguson and Hill 1922; Ferguson 1924; Hardy 1929).

Female (Plate 1, Fig. 2; and Part I, Plate 1, Fig. 5)

Close to *A. goldfinchi,* but more robust (length 19-22 mm), and to be separated by the following characters: Frons distinctly diverging; callus larger and extending above the middle of the frons (Fig. 4A); palpi wider. Scutum with a well-defined pair of median dark brown lines, sometimes fused, and an extensive dark brown sublateral stripe which is interrupted by the suture (see Part I, Plate 1, Fig. 5). Wings with costal cell yellow, and yellowish suffusion along veins; apex and posterior margin grey. Dark bands on abdominal tergites wider, their paler apical parts densely covered with bright golden hairs; paler areas on sternites reduced to narrow apical zones; apical fringes bright on 2nd to 4th sternites, dark golden more distally.
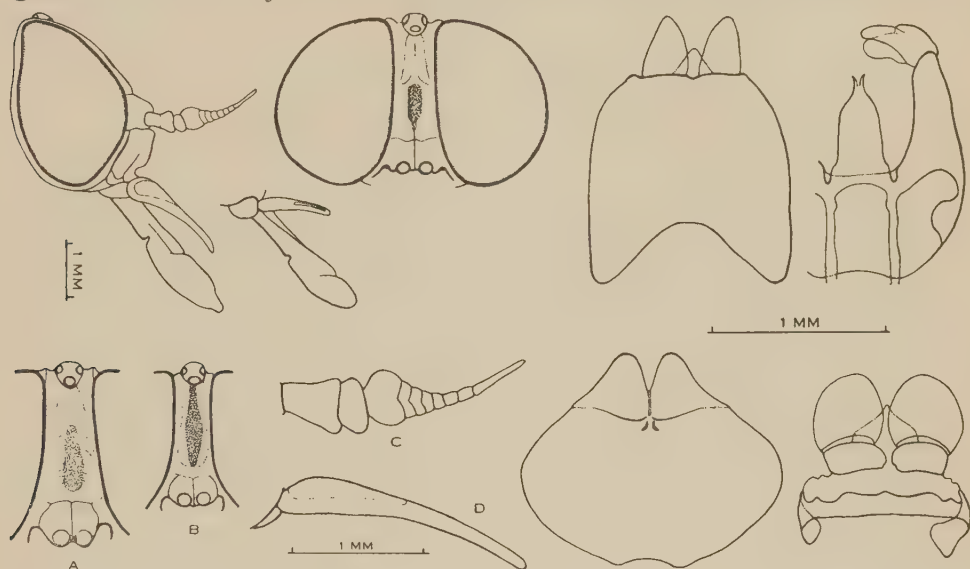
Fig. 4.—*Austroplex goldfinchi* Mack., head of ♀, proboscis and palp of ♂, genitalia of ♂ and ♀. *A, C,* frons and antenna of *A. chrysophilus* (Walk.), ♀; *B, D,* frons and palp of *A. brevipalpis* (Macq.), ♀.

Distribution.—QUEENSLAND: Wide Bay; Bribie I., Dec., Hacker; Toorbul Pt., Jan., at light, Marks. NEW SOUTH WALES: Richmond R. (Ferguson 1922); Broadwater, Clarence R., Nov., North; Lismore, Dec., Jan.; Lane Cove, Roseville and Wahroonga, Sydney, Jan., Froggatt, Taylor, Gibbons, Ferguson.

Genus ECTENOPSIS Macquart

Ectenopsis Macquart, 1838, p. 111; Loew 1860, p. 15 (as synonym of *Silvius*); Ricardo 1901, p. 287 (as synonym of *Silvius*), 1915c, p. 266; Surcouf 1921, p. 107; Enderlein 1922, p. 343, 1925, p. 314; Ferguson 1926a, p. 300; Mackerras 1955a, p. 469. Originally monotypic for *Chrysops vulpecula* Wiedemann, 1828, from unknown country (now known to be Australia).

Corizoneura Enderlein 1922, p. 337, 1925, p. 271, nec Rondani, 1863 (genotype erroneously designated as *Pangonia angusta* Macquart). Synonymy by Ferguson 1926a, p. 294.

This is a group of primitive flies, which lack the special features of *Austroplex, Caenoprosopon*, and *Therevopangonia*. It can be defined most conveniently by the characters of its subgenera separately. *Ectenopsis* can be used for the basic definition, and the others then distinguished more briefly by their differentiating features. There is one other subgenus (*Paranopsis*, in New Zealand), which combines the long palpi and bare eyes of *Ectenopsis* with the compacted 3rd antennal segment of *Parasilvius*. *E.* (*P.*) *victoriensis* is also intermediate between the two subgenera, but generally little difficulty should be experienced in separating them. The Chilean-Argentinian *Protodasyapha* and *Chaetopalpus* seem, on present evidence, to be closer to the Nearctic *Apatolestes* than to the Australian members of the group.

Subgenus ECTENOPSIS Macquart

Taxonomic details as above.

Female

Slender, smooth-bodied species. Eyes bare. Ocellar tubercle moderately developed. Frons wide (index about 2), diverging, more or less longitudinally furrowed, without callus. Subcallus small, tomentose, without hairs. Parafacials narrow; face convex from side to side, but appearing truncate in profile. First and 2nd antennal segments with short hairs; 3rd subulate, clearly 7- or 8-annulate, basal annulus about as wide as 2nd segment, and distal annuli not unusually slender. Palpi somewhat flattened, more than half the length of the shaft of the proboscis. Proboscis about equal to head height, stout, with large, soft labella. Hind tibial spurs of medium size. Cerci rounded apically; gonopophyses small; caudal ends of spermathecal ducts moderately chitinized, long, and slender.

Male

Eyes large, contiguous; upper facets not or slightly enlarged. Third antennal segment more slender than in ♀; palpi somewhat shorter. Hypopygium with aedeagus smooth; flagella small-medium; style with dorsal lobe slender, finger-like, ventral lobe swollen.

The adults haunt low vegetation, and a few have been taken on flowers. The life-history of *E.* (*E.*) *angusta* has been described by English (1953). The distribution of the subgenus is shown in Figure 2*A*, the record from Moa I. in Torres Strait being from a male, which was unfortunately destroyed, except for the mounted genitalia, before it had been fully identified.

The three forms that occur in eastern Australia present an interesting problem. *E.* (*E.*) *vulpecula* has a uniformly mustard yellow body, whereas *australis* is brown, with a banded abdomen. The female of *angusta* is yellowish, and tends to intergrade with *vulpecula,* but the male is brown, and merges into *australis*. There is no intergrading between

the males of *vulpecula* and *angusta,* nor between the females of *angusta* and *australis.* Analysis of the material available supports the opinion that the sexes of *angusta* are correctly allied. The three forms are not geographically separable, and it seems appropriate, therefore, to treat them as separate species, although the possibility of natural hybridization cannot be completely ignored.

KEY TO SPECIES OF THE SUBGENUS ECTENOPSIS

Females

1.   A brown species, with abdomen distinctly banded with grey, and usually with evident scutal vittae ....*australis* Ric.
     Yellow or light fawn, concolorous species, abdomen with at most obscure paler bands 2
2.   Mustard yellow species, with black legs, and blackish fore border to the wing ....*vulpecula* (Wied.)
     Paler yellow or fawn-yellow species, with at least the femora yellowish to light brown, and the fore border of the wing not markedly darkened ....
     ....*angusta* (Macq.)

Males

1.   A small (10 mm), dark species; basal segments of antennae with very long hairs; face sunken, very hairy; style of hypopygium as in Figure 5*D*; Western Australia ....*occidentalis*, sp. nov.
     Slightly larger (11-13 mm), not such dark species; basal segments of antennae with short hairs; face normal, moderately hairy; style of hypopygium as in Figure 5; eastern Australia 2
2.   A mustard yellow species, with black legs, and fore border of wings black ..
     ....*vulpecula* (Wied.)
     Brown species, with brown legs and fore border of wings brown 3
3.   Paler bands at apices of abdominal tergites, if present, yellowish and obscure
     ....*angusta* (Macq.)
     Paler bands at apices of abdominal tergites grey and conspicuous ..*australis* Ric.

Note.—If *Ectenopsis* (*Parasilvius*) *victoriensis* is incorrectly placed subgenerically, it will run down to *australis,* and be separable by the hairy eyes, and the 3rd antennal segment more swollen at base and with fewer than 8 annuli.

ECTENOPSIS (ECTENOPSIS) VULPECULA (Wiedemann)

Chrysops vulpecula Wiedemann, 1828, p. 195; Walker 1848, p. 205, 1854, p. 147. Type, sex not indicated, from unknown country, stated to be in the Berlin Museum.

Ectenopsis vulpecula (Wiedemann). Macquart 1838, p. 111; Ricardo 1915*c*, p. 266; Ferguson 1916, p. 205, 1921*b*, p. 10; Surcouf 1921, p. 108; Enderlein 1925, p. 314. Not Taylor 1918, p. 63, Ferguson 1922, p. 184, Hardy 1939, p. 41 (mis-spelt *vulpecuna*); all three should be referred to *angusta* (Macq.).

Silvius vulpecula (Wiedemann). Loew 1860, p. 15; Ricardo 1901, p. 297.

Ectenopsis vulpecula var. *nigripennis* Taylor, 1918, p. 63; Enderlein 1925, p. 315. Type ♀, from Norton's Basin, Nepean R., N.S.W., in the Australian

Museum, Sydney. Synonymy by Ferguson 1921*b*, p. 11. Following Miss Ricardo, Taylor regarded the duller coloured form (*angusta* (Macq.)) as typical, and the present form as a variety. Ferguson clarified their identity.

Material examined.—2 ♂ ♂, 6 ♀ ♀.

A uniformly mustard yellow species, with black legs, and greyish wings blackened along fore border. Length: 11-13 mm.

Female

Head.—Frons hollow in centre, uniformly covered with mustard yellow tomentum, without hairs. Subcallus and parafacials similar, without hairs, except for extreme lower margin of parafacials; face darker, with short, scattered, brown hairs. Basal segments of antennae brownish yellow, with black hairs; 3rd with basal annulus reddish brown, remainder darkening to brownish black on apical 4 annuli, the last relatively broad and rounded at tip. Palpi mustard yellow, darkening to brown apically, 1st segment with mixed dark brown and golden hairs, 2nd with short, dense, dark brown hairs. Beard scanty, creamy golden.

Thorax.—Scutum and scutellum mustard yellow, sometimes with faint indications of narrow, paler, median and dorsocentral lines; hairs on disc short, inconspicuous, yellow, longer and darker laterally in front of suture. Pleurae mustard yellow, with short, rather inconspicuous hairs below and in front of the anterior spiracle, on the posterior part of the upper mesopleural convexity, and on the hypopleural convexity.

Legs.—Coxae mustard yellow, a little paler than the general coloration; all remaining segments brownish black to black, contrasting strongly with the body colour.

Wings.—Darker than in related species; costal cell dark brown; vein R_1 brownish black; other veins dark brown; stigma dark brown. The effect of the very dark costal cell, radial vein, and stigma is to give the fore border of the wing a blackish appearance.

Abdomen.—Mustard yellow, with short yellow hairs fairly uniformly distributed on the tergites; sternites somewhat duller, with yellow-gold hairs, which are most evident towards their apical edges.

Male

Similar to ♀ in colour and markings, but more hairy. Eyes large; face with a mixture of golden and brownish hairs; hairs on 2nd segment of the palp long and dark.

Distribution.—QUEENSLAND: Brisbane (no other data). NEW SOUTH WALES: Roseville, Sydney, Dec., on *Bursaria*; old specimens in Macleay Museum labelled "N.S.Wales" or "Sydney", without other data.

ECTENOPSIS (ECTENOPSIS) ANGUSTA (Macquart)

Pangonia angusta Macquart, 1847, p. 11; Walker 1848, p. 144. Type ♂, from Australia, in the British Museum (Natural History).

Corizoneura angusta (Macquart). Ricardo 1900a, p. 113, 1915c, p. 266 (as synonym of *vulpecula* Wied.); Surcouf 1921, pp. 134 (also 107, 108 as synonym of *vulpecula* Wied.); Enderlein 1925, p. 271.

Ectenopsis vulpecula var. *angusta* (Macquart). Ferguson 1921b, p. 11; English 1953 (larva and pupa).

Corizoneura angusta Bigot, 1892, p. 617; Ricardo 1900a, p. 114, 1915c, p. 266 (as synonym of *vulpecula* Wied.); Froggatt 1911, p. 12. Type ♀, from Australia, in the British Museum (Natural History). Synonymy by Ferguson 1921b, p. 11.

Corizoneura rubiginosa Bigot, 1892, p. 617; Ricardo 1900a, p. 114, 1915c, p. 266 (as synonym of *vulpecula* Wied.); Froggatt 1911, p. 12; Enderlein 1925, p. 271. Type ♂, from Australia, in the British Museum (Natural History). Synonymy by Ferguson 1921b, p. 11.

Corizoneura bigoti Enderlein, 1925, p. 271, nom. nov. for *angusta* Bigot nec Macquart. Synonymy by Ferguson 1926a, p. 303.

Macquart's species has successively been regarded as a synonym of *vulpecula* (Wied.) by Miss Ricardo, a variety of *vulpecula* (Wied.) by Ferguson, and a distinct species in the present paper. The above names all apply to it.

Material examined.—26 ♂ ♂, 30 ♀ ♀.

A dimorphic species, which may account for some of the confusion in its identity. The female resembles *E. (E.) vulpecula*, but is paler, more fawn-yellow, with all wing veins brown, and at least the femora yellowish brown. The male can usually be distinguished from *E. (E.) australis* by its more uniformly coloured abdomen, with the apices of the tergites at most brownish yellow. Length: 10-13 mm.

Female (Plate 1, Figs. 4, 5)

Head.—Frons slightly narrower and duller than in *vulpecula*. Subcallus, parafacials, and face concolorous with frons, the face with short, brown to golden hairs. Basal segments of antennae creamy yellow, with black hairs; 3rd with basal annulus light orange, the next 2 or 3 darkening slightly, and the apical 4 dark brown, 8th longer and narrower than in *vulpecula*. Palpi about equal in length to the shaft of the proboscis, slightly paler than in *vulpecula*; 2nd segment with short, strong, dark brown hairs. Beard creamy.

Thorax.—Scutum and scutellum yellow with a hint of fawn, evenly covered with very short, inconspicuous, light brown to golden hairs; marginal hairs weak, dull to pale golden in front of suture. Pleurae creamy yellow, greyish between bases of coxae, and with fine, inconspicuous, light golden hairs.

Legs.—Coxae and femora creamy yellow to yellowish brown, with short creamy hairs; hind femur slightly darker than the others, and with dark brown hairs distally; fore and mid tibiae and tarsi brownish yellow, those of hind legs brown, all with brown to dark brown hairs.

Wings.—Uniformly greyish, with costal cell and all veins brown; stigma pale; the wing does not show the blackened fore border seen in *vulpecula*.

Abdomen.—Dull yellowish with a brownish hue, and with short brown and golden hairs on disc, longer creamy gold ones at margins. Venter brownish yellow, irregularly darker on some segments, and with fine, yellowish cream hairs.

This description is based on southern specimens. Those from north Queensland approximate more to *vulpecula*, the costal cell and radial vein sometimes being quite dark, and the tibiae, tarsi, and occasionally the apices of the femora dark brown. The only male so far seen from the far north has been *angusta*. In some specimens, the sublateral areas of the abdomen are variably stained with brown and covered with black hairs, but the general coloration is much more yellowish than in *australis*.

Male

Darker than ♀. Frontal triangle, face, and palpi brownish yellow, the palpi with long cream and brown hairs. Antennae similar to ♀. Scutum and scutellum brown, with the pronotal lobes light fawn, and variably developed yellowish brown dorsocentral lines and lateral areas; hairs brown, longer, and denser than in ♀. Pleurae more greyish than in ♀, with longer, denser, silky, creamy hairs. Legs and wings as in ♀. Abdomen brown, sometimes with indefinite brownish yellow apices to the tergites; with dark brown hairs on the disc, yellowish cream ones at apices of tergites, and relatively long and fine, but fairly dense, creamy lateral hairs, which extend variably on to the disc. Venter light yellowish brown, with mainly yellowish cream hairs.

Distribution.—QUEENSLAND: Cape York; Gordonvale, Dodd; Palm I., Dec., M. & M.; Rockhampton; Eidsvold, Bancroft; Brisbane, Nov., Feb., Mar., Hacker; Moggil, Apr.; Sunnybank, Oct., Perkins. It is possible that the specimen from Moa I., Jan., mentioned earlier, also belongs here. NEW SOUTH WALES: Maclean, Clarence R., Nov., on bush; Barrington Tops, Jan., S.U. Zool. Exp.; Kincumber, Dec., Davis; Gosford, Taylor; Woy Woy, Mar., Nicholson; Broken Bay, Dec., I.M.M.; Narrabeen, Dec., Day, Waterhouse; Woolwich, Sydney, Dec.-Jan., English; Sydney; Sylvania, Feb., D. F. Waterhouse; Cronulla, Jan., Gay; National Park, Jan., I.M.M.

ECTENOPSIS (ECTENOPSIS) AUSTRALIS Ricardo

Ectenopsis australis Ricardo, 1917, p. 217; Ferguson 1920, p. 132, 1921*b*, p. 12, 1922, p. 184; Surcouf 1921, p. 108; Enderlein 1925, p. 315. Type ♂, from Milson I., N.S.W., in the British Museum (Natural History); type ♀, from Sydney, N.S.W., in the Australian Museum, Sydney. Not Taylor 1918, p. 63 (misidentification of an undetermined species, according to Ferguson 1921*b*).

Material examined.—10 ♂ ♂, 10 ♀ ♀.

A brown species, with well-defined greyish fawn apical bands on the abdominal tergites, light to medium brown legs, and greyish wings not conspicuously darkened on fore border. Length: 11-14 mm.

Female (Part I, Plate 1, Fig. 4)

Head.—Frons often slightly narrower than in *angusta*, light to creamy fawn, with some short, inconspicuous, dark hairs at sides. Sub-

callus, parafacials, and face similar, lower part of parafacials and the face with dark brown hairs. Antennae as in *angusta*. Palpi yellowish cream to fawn, with dark brown hairs. Beard cream.

Thorax.—Scutum brown; in perfect specimens the median area is not as dark as the sublateral, there is a fine dark median line with narrow pale edges, well-developed greyish dorsocentral lines, which widen posteriorly, and greyish lateral areas; pronotal lobes greyish to fawn. Hairs short, inconspicuous, brown; marginal hairs weak, those in front of suture brownish, sometimes dark. Scutellum brown, sometimes greyish laterally, and with fine, light brown hairs. Pleurae pale fawn-grey, with creamy hairs.

Legs.—Coxae grey, with creamy hairs; fore and mid femora light to somewhat yellowish or creamy brown, with mixed pale and dark hairs; hind femora somewhat darker; tibiae and tarsi brown, with dark brown hairs.

Wings.—Costal cell brown; veins light to medium brown; stigma brown.

Abdomen.—Brown, with well-defined greyish fawn apical bands, often widening in the centre to form median triangles on some segments; hairs brown on the darker part, creamy on the paler areas; lateral margins with short creamy hairs. Venter light creamy brown, with paler apices to the sternites, and short creamy hairs.

Male

Similar to ♀, but slightly darker, and more hairy. The frontal triangle, face, and parafacials tend to an ashy hue, but vary towards the yellowish colour seen in the ♂ of *angusta*. Palpi shorter than in ♂ of *angusta*, with the basal segment usually more swollen, the 2nd more tapering, and the hairs on it darker; the form is transitional to that seen in *Parasilvius*. Beard well developed, greyish cream. Apical bands on abdominal tergites well defined, but sometimes narrower than in the ♀.

Distribution.—QUEENSLAND: Stanthorpe, Dec.-Feb., Perkins, Burns; Eukey, Jan., Wilson. NEW SOUTH WALES: Woy Woy, Mar., Nicholson; Mosman, Sydney, Dec., I.M.M.; Northbridge, Sydney, Nov., Fuller; Sydney, Dec., Nicholson, Jan., Ferguson; National Park, Jan., I.M.M.

ECTENOPSIS (? ECTENOPSIS) OCCIDENTALIS, sp. nov.

Type.—Holotype ♂, from King George Sound, W.A., in the Australian Museum, Sydney.

This species shows so many unusual features that it is felt desirable to describe it on a single specimen; a separate subgenus may be needed for it when it is sufficiently known.

Male

Resembles *E. (E.) australis*, from which it is to be distinguished as follows: Smaller (length 10 mm), darker, a deep greyish brown, but with

similar pale apical bands on the abdominal tergites. Face hollow; hairs on face and parafacials creamy white, long, and dense. Basal segments of antennae rather swollen, with very long hairs, which are more than twice the diameter of the segments; 3rd relatively short, dark brown, except at extreme base. Palpi short, conical, as in subgenus *Parasilvius*, covered with long cream and brown hairs. Proboscis slender, with small labella. Beard long, dense, cream. Pleurae and coxae grey. All femora brownish yellow, darkening somewhat apically on hind pair; hind tibiae little darker than others. Wings greyish, lightly suffused with brown on fore border. Style of hypopygium (Fig. 5D) broad and shaped rather like a bird's head; except for being bilobed, it is reminiscent of the style of *Phibalomyia* (Chrysopinae).

Distribution.—WESTERN AUSTRALIA: King George Sound.
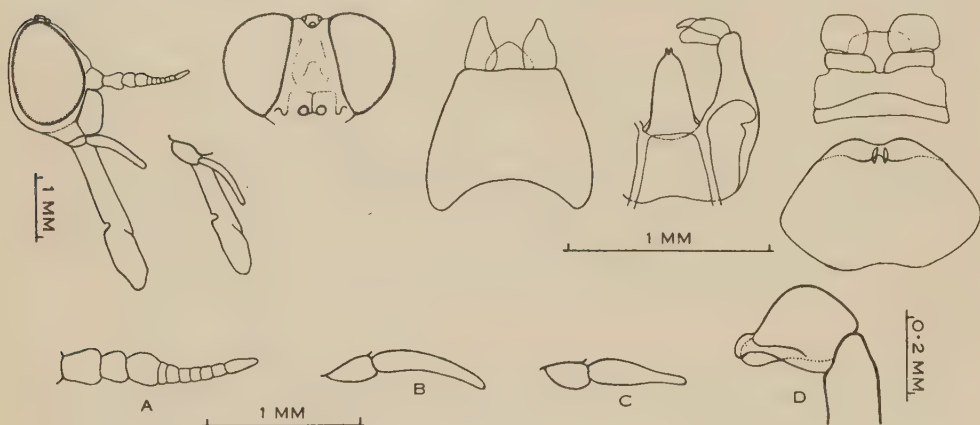
Fig. 5.—*Ectenopsis (Ectenopsis) vulpecula* (Wied.). *A*, antenna of ♀; *B*, palp of *E.* (*E.*) *angusta* (Macq.), ♂; *C*, palp of *E.* (*E.*) *australis* Ric., ♂; *D*, style of *E.* (?*E.*) *occidentalis*, sp. nov., ♂.

Subgenus PARASILVIUS Ferguson

Parasilvius Ferguson, 1921*b*, p. 8, 1926*a*, p. 300; Mackerras 1955*a*, p. 472. Originally monotypic for *Parasilvius fulvus* Ferguson, 1921, Victoria.
Ommia Enderlein, 1922, p. 348, 1925, p. 339. Monotypic for *Ommia prisca* Enderlein, 1925, Victoria. Ferguson (1926*a*, p. 305) could not place *O. prisca* End. other than as a synonym of *Ectenopsis? victoriensis* Ferg.; I concur.

Female

Parallel-sided species of medium build. Eyes with short, fine hairs, usually visible at × 20. Ocellar tubercle moderately developed. Frons usually rather narrower than in *Ectenopsis*, without callus. Face convex. Third antennal segment swollen at base, wider than 2nd; basal 3 or 4 annuli more or less completely fused, apical 4 clearly defined. Palpi short, usually awl-shaped. Proboscis relatively slender, with relatively small, firm labella. Hind tibial spurs medium. Cerci truncate apically.

Male

Smaller, more hairy, and with more tapering abdomen, than ♀. Hairs on eyes longer, but sometimes sparse; upper facets variably enlarged. Palpi similar, but with longer hairs.

The hairiness of the eyes varies considerably, from almost bare in both sexes of *fusca* to almost as hairy as *Scaptia* in the male of *fulva*. Reduction of the annuli of the 3rd antennal segment is also variable. In *fulva* and *fusca,* the segment is sometimes unequivocally 5-annulate, but more often shows traces of basal annulations as indicated in Figures 6C,
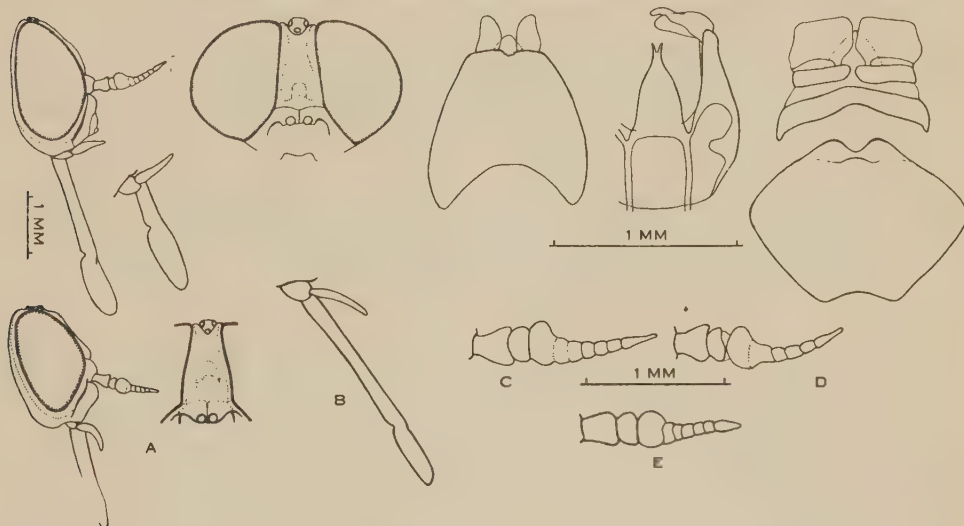
Fig. 6.—*Ectenopsis (Parasilvius) fulva* Ferg. *A,* head of *E. (P.) victoriensis* Ferg., ♀; *B,* proboscis and palp of *E. (P.) hamlyni* (Tayl.), ♂; *C,* antenna of *E. (P.) fulva,* holotype ♀; *D,* antenna of *E. (P.) fusca,* sp. nov., ♀; *E,* antenna of *E. (P.) victoriensis,* ♀.

6D. *E. (P.) victoriensis* lies almost midway between *Ectenopsis* and *Parasilvius* in habitus, and in the shape of the 3rd antennal segment, which is usually 6- or 7-annulate (Fig. 6E); I have placed it here on account of its perceptibly hairy eyes and short palpi.

There are no records of behaviour or life-history. The distribution is predominantly southern (Fig. 2B).

KEY TO SPECIES OF THE SUBGENUS PARASILVIUS
Females

1. A fulvous species, with rich yellow pleural hairs, and yellowish legs ......
   ....*fulva* Ferg.
   Brown species, with dull cream to brown pleural hairs, and brownish legs 2
2. A uniformly dark brown species, with almost bare eyes, relatively long proboscis, and shining, unbanded abdomen ....*fusca,* sp. nov.
   A lighter brown species, with distinctly hairy eyes, short proboscis, and tomentose abdomen with pale apical bands on the tergites ....*victoriensis* Ferg.

Males

1. Paler species, with greyish fawn scutum, and yellowish basal abdominal
       tergites 2
    Brown, more uniformly coloured species 3
2. A larger species (12-13 mm), with sparse hairs on eyes, and long, slender,
       clearly visible palpi ....*hamlyni* (Tayl.)
    A smaller species (10-11 mm), with densely hairy eyes, and short, less slender
       palpi hidden in long hair ....*fulva* Ferg.
3. A darker species, with almost bare eyes, and unbanded abdomen ..*fusca*, sp. nov.
    A lighter brown species, with perceptibly hairy eyes, and pale apical bands on
       abdominal tergites ....*victoriensis* Ferg.

ECTENOPSIS (PARASILVIUS) FULVA Ferguson

Parasilvius fulvus Ferguson, 1921*b*, p. 9. Type ♂ and ♀, from Sea Lake, north-
western Victoria, in the National Museum, Melbourne.

Material examined.—2 ♂ ♂, 3 ♀ ♀.

A medium sized, predominantly brownish yellow species, with olive
scutum covered with golden hair, yellow and brown abdomen, slightly
greyish wings, and yellowish legs. Length : ♀ 12-15 mm, ♂ 10-11 mm.

Female

Head.—Eyes with short and fine but fairly dense hairs. Frons
diverging, slightly hollow in centre, longitudinally wrinkled, covered with
yellowish fawn tomentum ; a small patch of short hairs on either side
below the middle. Subcallus pale yellowish fawn, somewhat creamy above
antennae. Parafacials pale creamy fawn, with inconspicuous, creamy
yellow hairs on lower half; face similar, with rather long, fine, creamy
hairs. Antennae: basal segments yellowish cream, with creamy yellow
hairs; 3rd orange, terminal annulus dark brown. Palpi yellowish fawn,
with creamy gold hairs, and dark brown ones distally. Proboscis slightly
longer than head, of medium thickness; labella large. Beard creamy gold.

Thorax.—Scutum olive over most of disc, yellowish along lateral
margins; the darker part covered with brown and golden hairs, the
lateral margins with fairly dense, light golden hairs. Scutellum similar
to disc, somewhat paler laterally ; with long brown and creamy gold hairs
centrally, entirely creamy gold ones laterally. Pleurae yellowish fawn
above, greyish below; with golden hairs on propleura and upper meso-
pleural convexity, greyish cream elsewhere.

Legs.—Femora bright yellow, with golden hairs; tibiae and tarsi
more yellowish brown, with dark brown hairs.

Wings.—Greyish, costal cell yellowish; veins yellowish basally, brown-
ish on rest of wing.

Abdomen.—Rather shining, light yellowish brown, a little variegated
in colour, and with fairly long and dense, uniform, dark brown hairs,
including the lateral margin. Venter light brownish yellow, with mixed
dark and creamy golden hairs.

Male

Similar to ♀, but smaller, more thick-set, somewhat paler, and much more hairy. Eyes densely hairy; palpi shorter and plumper than in ♀, and almost completely obscured by the parafacial hairs and beard.

In the types, the apical half or more of the abdomen is darker than the basal half, but they appear to be slightly greasy, and the abdomens of the other ♂ and ♀ are concolorous throughout.

Distribution.—VICTORIA: Sea Lake, Nov., Dec., Goudie; Mallee, Dec., Goudie.

ECTENOPSIS (PARASILVIUS) HAMLYNI (Taylor)

Caenoprosopon hamlyni Taylor, 1917*b*, p. 521; Surcouf 1921, p. 133; Enderlein 1925, p. 269. Type ♂, from Brisbane, October, in the Queensland Museum.

Corizoneura? *hamlyni* (Taylor). Ferguson and Hill 1922, p. 249 (also referred to as possibly *Buplex* or possibly *Pseudotabanus*).

Material examined.—5 ♂ ♂.

A yellowish species, with light greyish fawn scutum, creamy yellow abdomen marked with brown, light yellow legs, and faintly grey wings. To be distinguished from the ♂ of *fulva* by its larger size, sparse hairs on eyes, and much longer, slender palpi. Length: 12-13 mm.

Male (Plate 1, Fig. 6)

Head.—Eyes with long but sparse hairs; upper facets distinctly enlarged. Frontal triangle, subcallus, parafacials, and face covered with pale yellowish to fawn-cream tomentum, the parafacials and face with long creamy hairs. Basal segments of antennae yellowish cream, the 1st with creamy hairs except at the tip above, the 2nd somewhat darker and with black hairs; 3rd orange-yellow on its basal half, the distal 4 annuli blackish brown. Palpi yellowish cream, with long creamy hairs, and some dark brown ones below and apically on 2nd segment. Proboscis slightly longer than head, rather slender. Beard yellowish cream.

Thorax.—Scutum and scutellum with pale creamy fawn tomentum overlying an olive-grey integument; hairs yellowish cream, tending to golden on side margins and above wing root. Pleurae ashy grey, with silky, creamy hairs.

Legs.—Femora yellow to creamy fawn, with creamy hairs, which are mixed with some dark ones antero-ventrally on the hind femur; tibiae and tarsi yellowish brown, the hind legs darker, and all with short black hairs.

Wings.—Faintly grey, costal cell yellowish brown; veins yellowish at base, brown more distally.

Abdomen.—Light creamy yellow basally; a brownish mark across the centre of 1st tergite, a broader but inconspicuous one on 2nd, and brown basal or sub-basal bands on subsequent tergites; the brown markings tend to be narrower or interrupted in the mid-line; hairs black on darker parts, yellowish cream elsewhere. Venter light creamy yellow to fawn, irregularly darkened across some of sternites; hairs fine, cream.

Distribution.—QUEENSLAND: Brisbane, Sept., Oct., Hacker. NEW SOUTH WALES: "Calumet", 26 miles N.E. of Binnaway, Nov., Musgrave; Bogan R., Nyngan, Dec., Armstrong.

ECTENOPSIS (PARASILVIUS) FUSCA, sp. nov.

Types.—Holotype ♀, from Kelmscott, W.A., 17.i.1936, K. R. Norris, and allotype ♂, from Ardrossan, S.A., 5.i.1951, H. M. Cane, in the Division of Entomology, C.S.I.R.O., Canberra.

Material examined.—4 ♂ ♂, 2 ♀ ♀.

A uniformly deep brown species, with the costal cell and legs also brown. To be distinguished from *E. (P.) victoriensis* by darker colour, almost bare eyes, longer proboscis and shorter palpi, and absence of scutal vittae and pale bands on the abdomen. Length: ♀ 15 mm, ♂ 11-12 mm.

Female (Plate 1, Fig. 3; and Part I, Plate 1, Fig. 6)

Head.—Eyes with very short, sparse hairs. Frons covered with deep brown tomentum, with a few short hairs below middle; there is a median, elongate, diamond-shaped area on the lower half, where the tomentum is thinner, which may represent an incipient callus, and which is flanked by a small, shiny depression on each side. Subcallus brown. Parafacials brown along eye margin, more creamy and with creamy hairs medially; face deep brown, with brown hairs. Antennae with basal segments yellowish brown, with dark brown hairs; 3rd brownish orange at base, blackish on apical 4 annuli. Palpi light brown; basal segment with creamy hairs below; 2nd with short but fairly dense black hairs. Proboscis a little longer than head, slender, labella smaller than in *fulva*. Beard yellowish cream.

Thorax.—Scutum and scutellum uniformly dark brown, with dark brown hairs. Pleurae similar, but with some creamy yellow hairs anteriorly and on lower sclerites.

Legs.—Brown, with dark brown hairs, the femora somewhat lighter than the other segments.

Wings.—Grey, costal cell brown; anterior veins dark brown, more yellowish brown at base and posteriorly.

Abdomen.—Distinctly shining; uniformly deep brown, except for faint indications of slightly paler apices of tergites; hairs, including marginal hairs, deep brown. Venter a somewhat brighter brown, with brownish golden hairs, most conspicuous at apices of sternites.

Male

Smaller than ♀, not so dark, not so shining, and with more evident indications of paler apices to the abdominal tergites. Eyes with sparse, inconspicuous hairs; upper facets somewhat enlarged. Basal part of 3rd antennal segment bright brown, apical annuli only somewhat darker, so there is little contrast. The males described by Ferguson (1921*b*) as possibly *victoriensis* from South Australia agree with these specimens.

Distribution.—WESTERN AUSTRALIA: Kelmscott, Jan., Norris; Kalamunda, Feb., R. E. Turner; no loc., Newman. SOUTH AUSTRALIA: Ardrossan, Jan., Cane.

ECTENOPSIS (PARASILVIUS) VICTORIENSIS Ferguson

Ectenopsis? victoriensis Ferguson, 1921b, p. 12, 1921a, p. 368 (this note ante-dates the original description). Type ♀, from Mallee, Vic., in the National Museum, Melbourne.

Ommia prisca Enderlein, 1925, p. 339. Type ♀, from Melbourne, Vic., stated to be in the Berlin Museum. Synonymy by Ferguson 1926a, p. 305.

Material examined.—2 ♂ ♂, 1 ♀.

A medium sized, brown species, with evident thoracic vittae, pale apical bands on the abdominal tergites, light brown legs, and faintly greyish wings. Length: ♀ 12 mm, ♂ 10 mm.

Female

Head.—Eyes with short and fine but quite dense hairs. Frons light creamy fawn, irregularly yellowish in centre, with some very fine, pale hairs below the middle. Subcallus pale creamy fawn. Parafacials pale creamy fawn, with fine creamy hairs; face a little darker, with short, rather inconspicuous, brownish yellow hairs. Antennae with basal segments light fawn-cream, with brown and some cream hairs; 3rd brownish orange at base, blackish on apical 4 annuli. Palpi short, light brownish yellow, with brown hairs. Proboscis short and labella fairly large, more like Ectenopsis than Parasilvius. Beard short, cream.

Thorax.—Scutum brown, with faint median line, well-developed greyish fawn dorsocentral lines which widen anteriorly and in front of scutellum, and greyish fawn lateral areas; hairs dull cream, brownish in places. Scutellum brown, with light brown hairs. Pleurae pale grey, with brownish yellow and some ashy hairs.

Legs.—Femora light yellowish brown, with pale hairs; remaining segments more definitely brown, and with dark hairs.

Wings.—Faintly greyish; costal cell brown; veins yellowish at base, brown elsewhere.

Abdomen.—Tergites brown, with grey apical bands, which widen somewhat in the mid-line and posteriorly until the 6th and 7th tergites are almost entirely grey; hairs brown on the darker part, dull cream on the paler areas and lateral margins. Venter yellowish cream, with short creamy hairs.

Male

Similar to ♀, but darker; eyes with longer, denser hairs, upper facets distinctly enlarged; palpi shorter; dorsocentral lines and lateral areas on the scutum less well defined; and abdomen more crisply marked with narrow pale apical bands on all segments.

Distribution.—VICTORIA: Mallee (Ferguson 1921b); Merrinee, near Mildura, Jan., Wilson; Mordialloc, Jan.; Inverlock, Jan., Wilson.

Females of *fusca* and *victoriensis* are quite distinct, but the males are difficult to separate. Table 1 should facilitate identification.

TABLE 1

Characteristic	*fusca* ♂	*victoriensis* ♂
Body colour	Darker brown	Lighter brown
Hairs on eyes	Difficult to detect	Easily seen at × 15
Third antennal segment	Brown and darker brown, not contrasting	Orange and blackish, contrasting
Pleural hairs	Usually largely brown	Mostly greyish to cream
Pale bands on abdomen	Incipient	Clearly defined

Subgenus LEPTONOPSIS Mackerras

Leptonopsis Mackerras, 1955a, p. 470. Subgenotype *Ectenopsis (Leptonopsis) vittata* Mackerras, 1955, Western Australia, by original designation.

An exaggerated *Ectenopsis*, but with very slender 3rd antennal segment, triangularly produced face, and the palpi and proboscis of *Parasilvius*.

Female

Eyes bare. Ocellar tubercle unusually raised and prominent. Frons wide (index less than 2), with a small, central callus. Face strongly produced to form a well-defined triangle in profile. Third antennal segment clearly 8-annulate, very slender, little more than half width of 2nd at base. Palpi very short, awl-shaped. Proboscis relatively long and slender, with relatively small, firm labella. Hind tibial spurs medium.

Male

Smaller and more slender than ♀. Eyes large, holoptic; upper facets variably, sometimes greatly, enlarged. Otherwise similar.

Nothing is recorded of the habits or life-history, other than that the flies seem to be almost restricted to the dry, sandy, coastal country of Western Australia. Too few females were available to justify sacrificing one to study the mouthparts.

KEY TO SPECIES OF THE SUBGENUS LEPTONOPSIS

A greyish species, with conspicuous, dark brown vittae on scutum and abdomen ....*vittata* Mack.

A light brown species, with grey dorsocentral lines on scutum, and a grey median vitta on abdomen ....*norrisi*, sp. nov.

ECTENOPSIS (LEPTONOPSIS) VITTATA Mackerras

Fig. 7

Ectenopsis (Leptonopsis) vittata Mackerras, 1955a, p. 471. Holotype ♀, from Ardingly, W.A., November, in the Division of Entomology, C.S.I.R.O.; allotype ♂, from Monte Bello I., W.A., Sept., in the British Museum (Natural History).

Material examined.—3 ♂ ♂, 4 ♀ ♀.

A brightly marked, grey species, distinguished from all other members of the genus by having a strongly vittate thorax, and a median brown stripe and lateral brown margins on the abdomen. Legs light creamy brown; wings vaguely darkened along the crossveins. Length: 10-12 mm.

Female (Plate 1, Fig. 11)

Head.—Ocellar tubercle grey, with long, black hairs. Frons covered with pale fawn-grey tomentum; there is a small, longitudinal, light brown callus, and some short dark hairs above the middle on either side. Subcallus, parafacials, and face pale fawn-grey, with dark hairs laterally on face and on lower part of parafacials. Antennae with basal segments yellowish cream, with short black hairs; 3rd reddish brown, darkening on apical 4 annuli. Palpi light creamy fawn, with white hairs on the basal segment, and long but fine black ones on the 2nd segment. Beard ashy white.
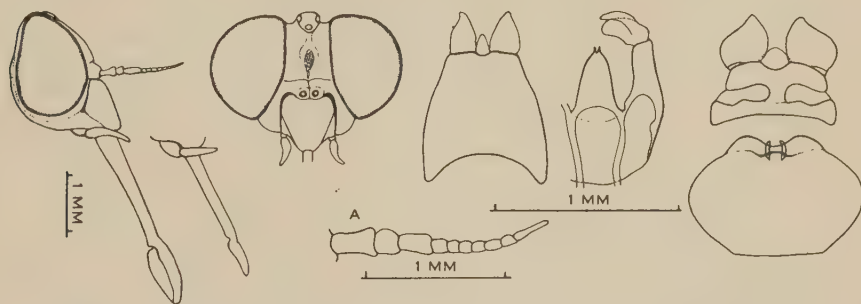
Fig. 7.—*Ectenopsis* (*Leptonopsis*) *vittata* Mack. *A*, antenna of ♀.

Thorax.—Scutum with narrow, continuous, dark brown median line lying on a lighter brown median area; the dorsocentral lines are strong, variably widened anteriorly and posteriorly, and ashy grey; and there is a wide ashy grey lateral area, so that the brown sublateral areas are reduced to broad vittae, which are interrupted at the suture, and do not reach the fore or hind margin; there is also a brown lateral spot above the wing root; hairs long but fine, brown. Scutellum grey laterally, brown in the median area, completing the appearance of a median brown stripe extending from the front of the thorax to the tip of the abdomen; hairs long, fine, mixed dark brown and greyish white. Pleurae light grey, with greyish white and brown hairs.

Legs.—Light fawn, with a little greyish tomentum on the femora. Hairs on femora greyish white, variably mixed with black; black on tibiae and tarsi.

Wings.—Greyish, with brown veins; somewhat suffused with brown anteriorly, and with narrow, rather vague, brownish clouds on *r-m*, the basal section of R_4 proximal to the appendix, the apex of the discal cell, and *m-cu*.

Abdomen.—Pale fawn-grey, with a broad, brown, median stripe, which is narrowly interrupted at the apices of some tergites, and with brown lateral patches on each tergite; hairs short, mixed black and cream; marginal hairs ashy white. Venter very pale fawn-grey, with the apices of the sternites creamy grey, and with short, pale hairs.

Male

Similar to ♀, but smaller, more hairy, and the darker scutal vittae not so complete. Eyes large, contiguous, bare; upper facets distinctly enlarged, but not sharply separated from the small lower and lateral facets. Palpi shorter than in ♀.

Distribution.—WESTERN AUSTRALIA: Monte Bello I., Sept., H.M.S. "Campania"; Ajana, Oct., Calaby; Northampton, Nov., A. J. Turner; Ardingly, Oct., Calaby.

ECTENOPSIS (LEPTONOPSIS) NORRISI, sp. nov.

Type: Holotype ♂, from Crawley, Perth, W.A., 29.xi.1939, K. R. Norris, in the Division of Entomology, C.S.I.R.O., Canberra.

This is a striking species, of which description is justified on a single specimen. It is light brown in colour, with paler scutal and median abdominal stripes, and distinctly spotted wings. Length: 12 mm.

Male

Head.—Wider than thorax; eyes markedly larger than in ♂ of *vittata*: upper facets unusually enlarged, 4 or 5 times as large as the lower, and sharply marked off from them. Frontal triangle, parafacials, and face pale creamy fawn, parafacials and face with fine brown hairs. Basal segments of antennae yellowish cream, with long black hairs; 3rd with basal 4 annuli orange, apical 4 dark brown. Palpi pale yellowish fawn, basal segment with long, silky, creamy white hairs, 2nd with long brown hairs. Beard creamy white.

Thorax.—Scutum and scutellum similar to *vittata,* but ground colour lighter brown, and dorsocentral vittae and lateral areas wider and paler grey, the general appearance being paler and less strongly vittate than in *vittata*; hairs long, fine, cream to brownish. Pleurae pale grey, with long, fine, creamy hairs.

Legs.—Light brownish yellow, darkening apically on tibiae and tarsi; femora with long, mixed creamy white and brown hairs; tibiae and tarsi with short, dark brown hairs.

Wings.—Greyish, with light brown veins, and lightly suffused with brown anteriorly. The brown spots are more distinct than in *vittata,* and there are indications of darker suffusion along some of the longitudinal veins, so that the centres of the cells are paler than their margins.

Abdomen.—Light yellowish brown, with narrow cream apices to 2nd and subsequent tergites, and a continuous, tomentose, brownish grey median stripe; hairs on disc brown and creamy white; marginal hairs

long, fine, creamy white. Venter pale fawn-cream, the apices of the ster-
nites cream; hairs creamy white.

Distribution.—WESTERN AUSTRALIA: Crawley, Perth, Nov., Norris.

Genus CAENOPROSOPON Ricardo

Caenoprosopon Ricardo, 1915c, p. 267; Surcouf 1921, p. 132; Enderlein 1925,
   p. 269; Ferguson 1926a, p. 300; Mackerras 1955a, p. 473. Originally monotypic
   for Caenoprosopon wainwrighti Ricardo, 1915 (= Corizoneura trichocera
   Bigot, 1892), New South Wales.

Demoplatus Ricardo, 1915c, p. 269; Surcouf 1921, p. 109; Enderlein 1925, p. 272.
   Genotype Corizoneura trichocera Bigot, 1892, Australia, by original designation.
   Synonymy by Ferguson 1926a, pp. 300, 304.

Cryptoplectria Enderlein, 1923, p. 544, 1925, p. 272. Monotypic for Demoplatus
   australis Ricardo, 1915, New South Wales. Synonymy by Ferguson 1926a,
   p. 300.

A primitive but aberrant genus, in which the females of only one
species are known. I have seen 25 males of the australis group, so the
absence of females is curious; they may possibly be apterous, or restricted
to some unsuspected habitat.

Female

Fairly large, rather elongate, soft-bodied flies, distinguished im-
mediately from all other Australian genera, except Therevopangonia, by
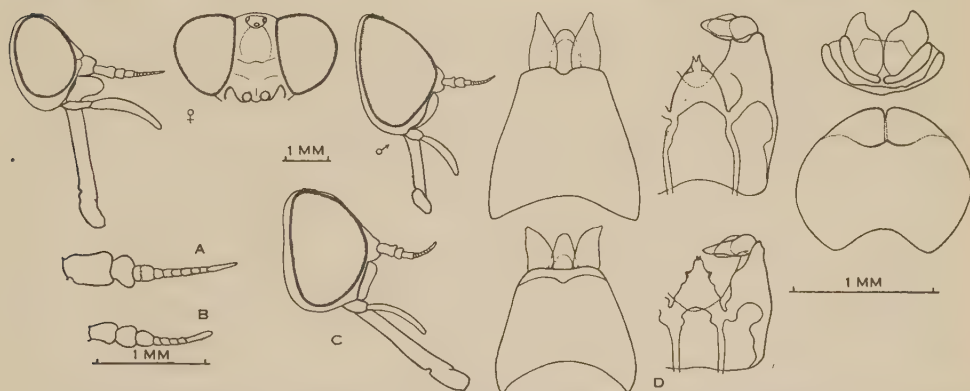
Fig. 8.—Caenoprosopon trichocerus (Big.). A, antenna of ♂; B, antenna of C. minor
   (Tayl.), ♂; C, D, head and hypopygium of C. australis (Ric.), ♂.

the projecting, hairy subcallus and strongly bulging face, the profile
being quite distinctive (Fig. 8). Eyes small, widely separated, bare.
Frons retreating, diverging, hollow in centre, longitudinally wrinkled,
without callus. Subcallus and face tomentose. First antennal segment
nearly twice as long as wide; 2nd normal; 3rd unusually small and
slender, considerably narrower than 2nd, and the number of annuli
varying from 8 (usual) down to 6 and occasionally 5. Palpi very long,
somewhat flattened, broadly sabre-shaped in lateral view. Proboscis

short, stout; labella well developed, soft; mandibles absent. Hind tibial spurs small or minute, sometimes not detectable. Eighth sternite large and rounded; 9th tergite widened laterally; caudal ends of spermathecal ducts of cleared specimens visible only by phase-contrast microscopy.

Male

Distinctly different from ♀, more slender, firmer-bodied, and with flat subcallus and face. Eyes large, contiguous; palpi generally similar to ♀, but not as long and usually not as wide in lateral view, occasionally quite slender. Hypopygium distinguished by the small, broadly triangular aedeagus, exceedingly small flagella, and broad, pointed dorsal lobe of the style.

Two groups can be recognized in the males:

trichocerus group: concolorous fawn to yellowish species; upper facets of eyes distinctly enlarged; palpi relatively small and slender (although they are exceedingly large in the female); lobes of style broader; sides of aedeagus with a small, inturned projection.

australis group: brown to blackish species; upper facets of eyes not at all enlarged; palpi longer, sabre-shaped; lobes of style, especially the dorsal, more slender; sides of aedeagus with sinuous margins and a pointed, outwardly-directed projection. Enderlein's name *Cryptoplectria* is available for this group, if separation proves to be desirable when the females are discovered.

The females are presumably incapable of sucking blood. Most specimens of both sexes have been collected on bracken and other low vegetation. Nothing is known of their life-history. The distribution is entirely coastal and highland in eastern Australia, except for a doubtful record from South Australia (Fig. 2C).

KEY TO SPECIES OF THE GENUS CAENOPROSOPON

Females

Only one known. Concolorous fawn to yellowish; wings vaguely marked with light brownish yellow, often with discrete darker spots at crossveins ....
....*trichocerus* (Bigot)

Males

1. A concolorous yellowish fawn to brown species; upper facets of eyes enlarged; wings as in ♀ ....*trichocerus* (Bigot)
   Brown to blackish species; upper facets of eyes not enlarged; wings more or less infuscated with dark brown anteriorly 2

2. A lighter coloured species, with brownish yellow scutellum, and almost uniformly bright brown abdomen ....*minor* (Tayl.)
   Darker species, with olive-brown scutellum, and dark, patterned abdomen 3

3. Abdomen blackish, with narrow pale apical bands on the tergites; brown markings on wings diffusing into ground colour ....*australis* (Ric.)
   Abdomen reddish brown, with a dark median vitta; brown colour of wing tending to form a more definite pattern ....*nigrovittatus* (Ferg. & Hill)

Caenoprosopon trichocerus (Bigot)

Corizoneura trichocera Bigot, 1892, p. 616; Ricardo 1900a, p. 114; Froggatt
  1911, p. 12. Type ♂, from Australia, in the British Museum (Natural
  History); allotype ♀, from Herberton, north Queensland, designated by
  Ricardo 1915c, stated to be in the German Entomological Museum, Berlin.

Demoplatus trichocerus (Bigot). Ricardo 1915c, p. 269; Ferguson 1916, p. 205,
  1921a, p. 368, 1922, p. 184, 1926a, p. 300; Surcouf 1921, p. 109; Enderlein
  1925, p. 272.

Caenoprosopon wainwrighti Ricardo, 1915c, p. 268; Taylor 1917b, p. 522; Ferguson
  1920, p. 132, 1922, p. 184, 1926a, p. 300; Ferguson and Henry 1920, pp. 830,
  838; Surcouf 1921, p. 133; Enderlein 1925, p. 269; Henry 1927, p. 195. Type
  ♀, from Blue Mts., N.S.W., in the British Museum (Natural History). The
  only distinctions I can find between *trichocerus* (Bigot) and *wainwrighti* Ric.
  are in the wing markings and the fawn or yellowish colour. There are
  intergrades in both characters in the series before me.

Material examined.—15 ♂ ♂, 12 ♀ ♀.

A concolorous, brownish yellow to fawn species; the females larger
than the males, and with soft, rather wrinkled abdomen; both sexes with
yellowish to light brown legs, the wings vaguely clouded with brown or
yellowish brown, and sometimes with discrete darker spots on the cross-
veins. The number of annuli in the 3rd antennal segment is extremely
variable, most frequently 8, but varying down to 6, and rarely 5. Length:
southern specimens, ♂ 13-14 mm, ♀ 14-18 mm; north Queensland speci-
mens, ♂ 10-12 mm, ♀ 11 mm.

Female (Plate 1, Figs. 7, 8)

Head.—Frons covered with mustard yellow to fawn-yellow tomentum,
without hairs. Subcallus slightly darker, with a group of brown hairs on
either side. Parafacials similar, without hairs, except at lower margin;
face more brownish yellow, rather densely covered with long brown hairs.
Basal segments of antennae light fawn-yellow, with dark brown hairs;
3rd orange to creamy yellow, with the apical 1 or 2 annuli darker. Palpi
with 1st segment and base of 2nd creamy yellow, with creamy yellow
and a few dark hairs, apical four-fifths of 2nd light yellowish brown,
with strong, dark brown hairs. Proboscis with shaft light to yellowish
brown, labella darker. Beard creamy gold, rather sparse.

Thorax.—Scutum and scutellum bright brownish yellow to fawn,
sometimes with indications of narrow, paler median and dorsocentral
lines; hairs short, creamy to brownish gold. Tegula and edge of pleurae
along lateral margin of notopleural and pronotal lobes brown, often dark,
forming a conspicuous line at junction between scutum and pleurae, which
are creamy yellow, with fine cream hairs.

Legs.—Creamy to light brownish yellow, with creamy golden hairs;
apical tarsi darker, with brown hairs.

Wings.—Slightly greyish, sometimes paler in centre of discal and
marginal cells, and with vague irregular darkening anteriorly and across

apices of basal cells. This form corresponds to *wainwrighti* Ric. In the *trichocerus* variant, there are, in addition to the more vague colouring, discrete brown spots covering *r-m*, the basal section of R_4, the apex of the discal cell, *m-cu*, and an inconstant but frequent spur, which projects forward into the lower part of the discal cell about its middle. The extent to which these spots are developed is variable.

Abdomen.—Reddish yellow to fawn, soft, rather wrinkled, with sparse, fine, creamy yellow hairs. Venter similar, but somewhat paler.

Male (Plate 1, Fig. 9)

Generally similar to ♀, but smaller, darker, and the abdominal sclerites more firmly chitinized. Upper facets of eyes distinctly enlarged. Third antennal segment more uniformly brownish yellow, only darkening slightly at tip. Palpi shorter and very variable in width, in some specimens quite broadly spatulate, with a small lateral bare area on distal half, in others thin and almost thread-like, and in others intermediate. Beard mixed creamy yellow and some dark brown hairs. Pleurae with brownish yellow to creamy white hairs. Legs and wings similar to ♀, but the vague infuscation is brown rather than yellowish brown. Abdomen yellowish fawn to brown, sometimes with paler apices to tergites; hairs brown and creamy gold to light cream, lateral fringe fairly well developed.

The series before me shows considerable variation in size and colour, as well as in wing markings. Three males and a female from north Queensland are smaller than southern specimens, and the anterior margin of the wing is more distinctly brown. They might possibly represent a distinct race, but I cannot find characters to justify separating them.

Distribution.—QUEENSLAND: Kuranda, Dodd (Ricardo 1915*c*); Cairns, Taylor; Herberton, Dodd (Ricardo 1915*c*); Mulgrave R.; Palm I., Dec., M. & M.; Brisbane, Apr., Philip; Mt. Tamborine, Nov., Feb., Davidson, Hacker, Lea; National Park, Nov., Hacker. NEW SOUTH WALES: Tooloom, Jan., Perkins; Kendall (Ferguson 1922); Eccleston, Jan., Hopson; Woy Woy, Mar., Nicholson; Milson I., June, resting on *Casuarina*; Blue Mts. (Ricardo 1915*c*); Blayney, Jan., Goldfinch; Wahroonga, Sydney, Mar., Nicholson; Killara, Sydney, Feb., Waterhouse; Roseville, Sydney, Mar., Ferguson; Epping, Sydney, Mar., in bush, Froggatt; Sydney, Gibbons, Taylor; Stanwell Park, Mar., Goldfinch; Illawarra.

CAENOPROSOPON AUSTRALIS (Ricardo)

Demoplatus australis Ricardo, 1915*c*, p. 270; Ferguson 1916, p. 205, 1917, p. 252, 1922, p. 184; Surcouf 1921, p. 109. Type ♂, from Katoomba, N.S.W., 3400 ft, in the British Museum (Natural History). Not Taylor 1917*b*, p. 521 (= *minor* (Tayl.)).

Cryptoplectria australis (Ricardo). Enderlein 1925, p. 272.

Material examined.—8 ♂ ♂.

A dark brown to blackish species, with apical paler bands on the abdominal tergites, bright yellowish brown legs, and anterior half of wing strongly infuscated with brown. Length: 11-14 mm.

Male

Head.—Frontal triangle, subcallus, parafacials, and face with pale creamy grey tomentum, the subcallus with a strong group of black hairs on each side, the parafacials with creamy white and a few brown hairs, and the face with long brown hairs. Basal segments of antennae brownish fawn, with some cream tomentum and long black hairs; 3rd bright, slightly reddish brown, darkening on apical annuli. Palpi with basal segment light greyish brown, with mixed creamy white and dark brown hairs; 2nd nearly as long as shaft of proboscis, sabre-shaped, densely covered with quite strong dark brown hairs. Proboscis with shaft dark greyish brown, with brown hairs on its whole length below; labella dark brown, hairy. Beard creamy white.

Thorax.—Scutum olive brown, with faint greyish brown dorsocentral lines; lateral margins paler, yellowish brown above and behind wing root; hairs fairly dense, brownish yellow, paler at sides, and dull golden above the wing root. Scutellum olive brown, with greyish margins, and fine cream hairs. Pleurae grey, with creamy white hairs.

Legs.—Coxae grey; remaining segments bright brownish yellow, except hind tibiae and tarsi, which are brown.

Wings.—Greyish, strongly suffused with brown in costal and radial area, with a tendency to leave the centres of the cells paler, and for a darker band to develop across the apices of the basal cells; the edges of the brown fade diffusely into the ground colour; appendix on R_4 variable, sometimes a mere stump.

Abdomen.—First tergite dull greyish brown; 2nd to 5th more blackish brown, a little lighter laterally; 6th bright brown, with a deep brown median patch; apical tergites bright brown; all with pale fawn-grey apical margins, most conspicuous on the 2nd to the 5th; hairs creamy white, long but fine, and fairly dense on the lateral margins. Venter bright orange-brown, apices of sternites paler, with brown and creamy white hairs.

Three specimens from Eccleston are smaller, somewhat lighter in colour, with diffuse brown markings on wings, but a tendency for the dark colour on the abdomen to be reduced to a vague median stripe on a brown ground. They suggest that *australis, nigrovittatus,* and possibly *minor,* may merge, when sufficient specimens are known.

Distribution.—NEW SOUTH WALES: Eccleston, Allyn R., Feb.; Gosford, Taylor; Woy Woy, Mar., Nicholson; Milson I., Hawkesbury R., Mar., Apr., on bracken and grass stem; Katoomba (Ricardo 1915c).

CAENOPROSOPON NIGROVITTATUS (Ferguson & Hill)

Demoplatus nigrovittatus Ferguson & Hill, 1920, p. 460; Ferguson 1922, p. 184; Enderlein 1925, p. 272. Type ♂, from Kendall, N.S.W., in the Australian Museum, Sydney.

Caenoprosopon nigrovittatus (Ferguson & Hill). Henry 1927, pp. 195, 196.

Material examined.—14 ♂ ♂.

Male (Plate 1, Fig. 10)

Distinguished from *C. australis* chiefly by the abdominal pattern. The tergites are bright reddish brown, with the paler apices obscure, and a median, interrupted, dark brown stripe along whole length of abdomen; the lateral margins are also darkened. The brown coloration of the wings is more extensive, and tends to form a more definite pattern. The shape of the apical edge of the 7th abdominal tergite, sinuous in *australis,* truncate in *nigrovittatus,* was thought by Ferguson and Hill to be an additional differentiating character, but it has proved to be variable in the specimens before me. Length: 9-13 mm.

Distribution.—QUEENSLAND: Halifax, Oct., Dormer; Palm I., Dec.-Jan., M. & M.; Mackay, Feb.; Eidsvold, Bancroft. NEW SOUTH WALES: Port Macquarie, Apr., Nicholson; Kendall (Ferguson and Hill 1920).

CAENOPROSOPON MINOR (Taylor)

Silvius minor Taylor, 1918, p. 62. Type ♂, stated to be from South Australia, in the Australian Museum, Sydney.

Ectenopsis? minor (Taylor). Ferguson 1921*b*, p. 11. Ferguson thought that a new genus might be necessary for this species, but it clearly belongs to the *australis* section of *Caenoprosopon* on shape, coloration, form of antennae and palpi, small upper facets of eyes, and genitalia.

Material examined.—7 ♂ ♂.

A brown species; disc of scutum dark brown, lateral areas and scutellum brownish yellow; abdomen almost concolorous brown; wing markings like *C. nigrovittatus.* Length: 11-14 mm.

Male

Head.—Like *C. australis,* but antennae paler; basal segments yellowish cream, with dark brown hairs; 3rd usually with 6 or 7 annuli.

Thorax.—Scutum dark to olive brown, with paler dorsocentral lines, and a wide but diffuse yellowish brown zone around lateral margins, on posterior edge of scutum, and whole of scutellum; hairs brownish to yellowish cream. Pleurae light fawn-brown, with darker brown patches on the lower anterior part of the upper mesopleural convexity and between the coxae; hairs yellowish cream, rather dull.

Legs.—Light brownish yellow, darkening apically on tarsi; femora with mixed brown and creamy hairs, remaining segments chiefly with short, fine, creamy hairs, except hind tibiae and apical tarsi of all legs, on which the hairs are predominantly brown.

Wings.—Greyish, suffused with brown anteriorly, and with well marked darkening at apices of basal cells and apex of discal cell, so that the wing tends to show a pattern like *C. nigrovittatus.*

Abdomen.—Brown; 1st tergite with a fawn tint; 2nd to 5th with pale apical margins which tend to widen to form incipient median triangles; hairs creamy. Venter paler than dorsum.

Distribution.—QUEENSLAND: Brisbane, Nov., Mar., Hacker; Gatton, Dec., G. L. Wilson; Beaudesert, Apr., I.M.M. ?SOUTH AUSTRALIA: Taylor saw two specimens, and recorded the type locality as South Australia, without further data. The paratype has no locality label, but Mr. A. Musgrave has informed me that both specimens are listed under one number in the Australian Museum Register as ?South Australia, from old collection material. As these are the only two specimens of the genus recorded from outside eastern New South Wales and Queensland, the locality must be regarded as doubtful.

Genus THEREVOPANGONIA Mackerras

Therevopangonia Mackerras, 1955a, p. 474. Monotypic for *Therevopangonia insolita* Mackerras, 1955, Western Australia.

Female

Exceedingly small (7-8 mm), parallel-sided, bristly, therevid-like species. Eyes small, very finely hairy. Frons exceedingly wide (index 1), diverging, tomentose, without central callus, but with a pair of oblique, narrow, shining, bare areas covering the junction with the wide, strongly projecting, otherwise tomentose subcallus. Face somewhat bulbous. Antennae with 1st segment somewhat swollen, a little less than twice as long as broad; 2nd rounded; 3rd wider than 2nd, swollen basally, and with a short, well-defined style; the basal part is either single, or divided into 2 or 3 indefinite annuli, and the style is clearly 3-annulate, so that the whole segment is 4-6-annulate. Palpi short, tapering, rather like *Parasilvius*, hairy. Proboscis about equal in length to head height, slender; labella small, chitinized; mandibles absent. Legs short, stout, bristly; hind tibial· spurs well developed. Eighth sternite intermediate in shape between *Ectenopsis* and *Caenoprosopon;* 9th tergite a broad, chitinized sclerite.

Male

Similar to ♀, but smaller. Eyes large, contiguous, finely hairy; facets on the upper four-fifths distinctly, though not greatly, enlarged. Subcallus not projecting, and face retreating, unlike that of ♀. Palpi smaller than in ♀. Ninth tergite strongly arched, notched apically; aedeagus smooth; flagella well developed but small; dorsal lobe of style slender, finger-like, as in *Ectenopsis,* ventral lobe large.

The outstanding features of the genus are the therevid-like facies, and the quite unusual form of the 3rd antennal segment. The only known species was collected in spring in dry country in Western Australia. Nothing is recorded of its habits or life-history.

THEREVOPANGONIA INSOLITA Mackerras
Fig. 9

Therevopangonia insolita Mackerras, 1955a, p. 475. Holotype ♀, from Geraldton, W.A., Sept., and allotype ♂, from Eradu near Geraldton, in the School of Public Health and Tropical Medicine, University of Sydney.

Material examined.—40 ♂♂, 8 ♀♀.

A very small, dark greyish to brown species; with short antennae; greyish scutum; stout, grey, and yellowish brown, bristly legs; greyish wings, with a well-defined stigma; and dark brown abdomen, with paler apical bands on the tergites. Length: ♀ 7-8 mm, ♂ 5-7 mm.

Female (Plate 1, Fig. 12)

Head.—Frons with greyish tomentum, a little darker on either side of a central, slightly depressed area; lateral parts with long brown and some creamy yellow hairs. Ocellar tubercle prominent, grey, bearing long dark hairs. Subcallus pale creamy grey below the shining dark brown band on each side. Parafacials wide, pale grey, with long brown and creamy yellow hairs. Face creamy grey, with inconspicuous creamy hairs. Antennae with basal segments light brownish grey, with long black hairs; 3rd yellowish brown at extreme base, remainder dark brown. Palpi short, subcylindrical, pale brownish grey, with very long brown and creamy hairs. Beard creamy, long but sparse.
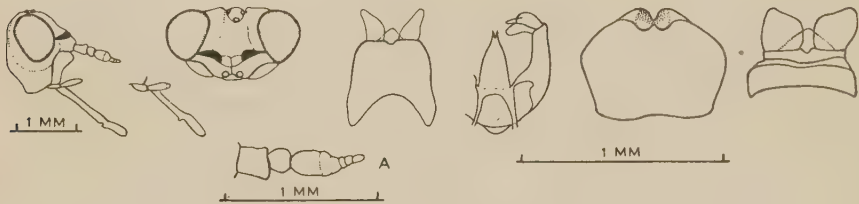
Fig. 9.—*Therevopangonia insolita* Mack. *A*, antenna of ♀.

Thorax.—Scutum dark grey, with indefinite lighter grey dorsocentral lines, pale grey shoulders, and grey lateral margins; hairs long, relatively dense, black or dark brown, rather conspicuous on presutural lateral area. Scutellum grey, with fine black hairs. Pleurae grey, with long dull creamy hairs and some dark ones on posterior edge of upper mesopleural convexity.

Legs.—Short and stout; fore and hind femora distinctly swollen. Coxae and femora greyish brown, with long, dull creamy and black hairs. Tibiae and tarsi yellowish brown, fore and mid with mixed bristly black to golden hairs, hind a little darker and with golden to brown hairs. Spurs on mid and hind tibiae and all claws unusually strong; empodium and pulvilli long and thin.

Wings.—Grey; veins dark brown; stigma dark brown, conspicuous.

Abdomen.—First tergite light grey, with brownish lateral patches, and pale creamy grey apical margin; remaining tergites dark brown, with pale greyish fawn apical margins; hairs not conspicuous, brown on the darker parts, yellowish cream on the paler areas and lateral margins. Venter light grey, with pale greyish cream hairs, and some black ones near apex of abdomen.

THE TABANIDAE (DIPTERA) OF AUSTRALIA. II

Male

Similar to ♀, but smaller and even more hairy. Head wide, but subcallus and face do not project as in ♀. Abdominal markings variable, some specimens being like ♀, while in others the grey colour predominates, the brown being reduced to form darker basal bands, sometimes interrupted in the median line, on tergites 2-4.

Distribution.—WESTERN AUSTRALIA: Geraldton and Eradu, Sept., Ferguson, Nicholson; Dongarra, Sept.-Oct., R. E. Turner.

EXPLANATION OF PLATE 1

Representative Australian Pangoniini. The scale is in millimetres. Photographs by M. J. Mackerras

Fig. 1.—*Austroplex brevipalpis* (Macq.), ♂.
Fig. 2.—*Austroplex chrysophilus* (Walk.), ♀.
Fig. 3.—*Ectenopsis* (*Parasilvius*) *fusca*, sp. nov., ♀.
Figs. 4 and 5.—*Ectenopsis* (*Ectenopsis*) *angusta* (Macq.), ♀.
Fig. 6.—*Ectenopsis* (*Parasilvius*) *hamlyni* (Tayl.), ♂.
Figs. 7-9.—*Caenoprosopon trichocerus* (Bigot), ♀, ♀, ♂.
Fig. 10.—*Caenoprosopon nigrovittatus* (Ferg. & Hill), ♂.
Fig. 11.—*Ectenopsis* (*Leptonopsis*) *vittata* Mack.
Fig. 12.—*Therevopangonia insolita* Mack.

LIST OF GENERA AND SUBGENERA

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